

## Seed Plant Genera Endemic to the Caribbean Island Biodiversity Hotspot: A Review and a Molecular Phylogenetic Perspective

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## Abstract

The Caribbean Island Biodiversity Hotspot is composed primarily of the Bahamas and Greater and Lesser Antilles. A total of 180 genera (727 spp., ca. 9% of the species endemic to the Antilles) are restricted to this hotspot. Most of these genera are unispecific (51%), a pattern that is also found on other islands of the world. The majority of the endemic genera belong to the “Core Eudicot” clade, and they were published in two time periods (1854–1878 and 1904–1928). There are molecular phylogenies available for 63 of the endemic genera. However, phylogenetic reconstructions of only 21 genera are based on more than one independent DNA region and have well-supported clades and good taxonomic sampling. Six of the endemic genera form part of early-branching groups. We could not infer biogeographical conclusions from the molecular phylogenies of most of the endemic genera (43: 68%). There is an urgent need for (1) additional field studies to learn the conservation status of these genera, (2) effective protection of the habitats where the most endangered genera occur, and (3) additional biological and systematic studies of the least understood genera.

## Introduction

### DEFINING THE CARIBBEAN ISLAND HOTSPOT—REVIEW OBJECTIVES

There is agreement among conservation biologists that the 34 currently recognized biodiversity hotspots harbor high levels of biodiversity in relatively restricted geographical areas (Mittermeier et al., 2004) and complement the terrestrial ecoregion concept of Olson et al. (2001). An understanding of the taxonomy of organisms that live in these hotspots is one of the initial steps needed prior to the establishment of management policies for the conservation of species and their associated habitats. The Caribbean Islands comprise one of these biodiversity-rich areas, in which clarification of taxonomic boundaries for plants remains a high priority task (Campbell & Hammond, 1989).

The Caribbean Islands are far from being biologically homogeneous. Their complexity is the result of intricate geological histories that vary among islands, the presence of diverse environments, the biological influence of species-rich continental areas, and differences in isolation degree (Santiago-Valentín & Olmstead, 2004). Therefore, it is not surprising that various boundaries have been proposed for this hotspot (Cincotta et al., 2000; Myers et al., 2000; Smith et al., 2004c). It was originally named the “Caribbean Hotspot,” and, in addition to the Caribbean Islands, also included the southern portion of Florida (Cincotta et al., 2000; Myers et al., 2000). A more recent definition by Smith et al. (2004c) excludes continental North America from this hotspot. The latest account of biodiversity hotspots (Mittermeier et al., 2004) defines the “Caribbean Island Hotspot” as composed of the Lesser and Greater Antilles, the Bahamas, and most of the islands located off the north coast of Venezuela (Smith et al., 2004c) (Fig. 1). In our paper we follow this most recent definition by Smith et al. (2004c) and exclude south Florida. Only 10 plant genera are shared exclusively by the Caribbean Islands and the southern tip of the Florida peninsula, and there are no genera endemic to this continental part of North America (Liu et al., 2004). The terms “Antilles” and “Caribbean Islands” are applied in this paper to the islands within the “Caribbean Island Hotspot” as indicated in Figure 1.

In this work, we characterize the genera of seed plants endemic to the Caribbean Island Hotspot sensu Smith et al. (2004c). Our review is a first step toward understanding

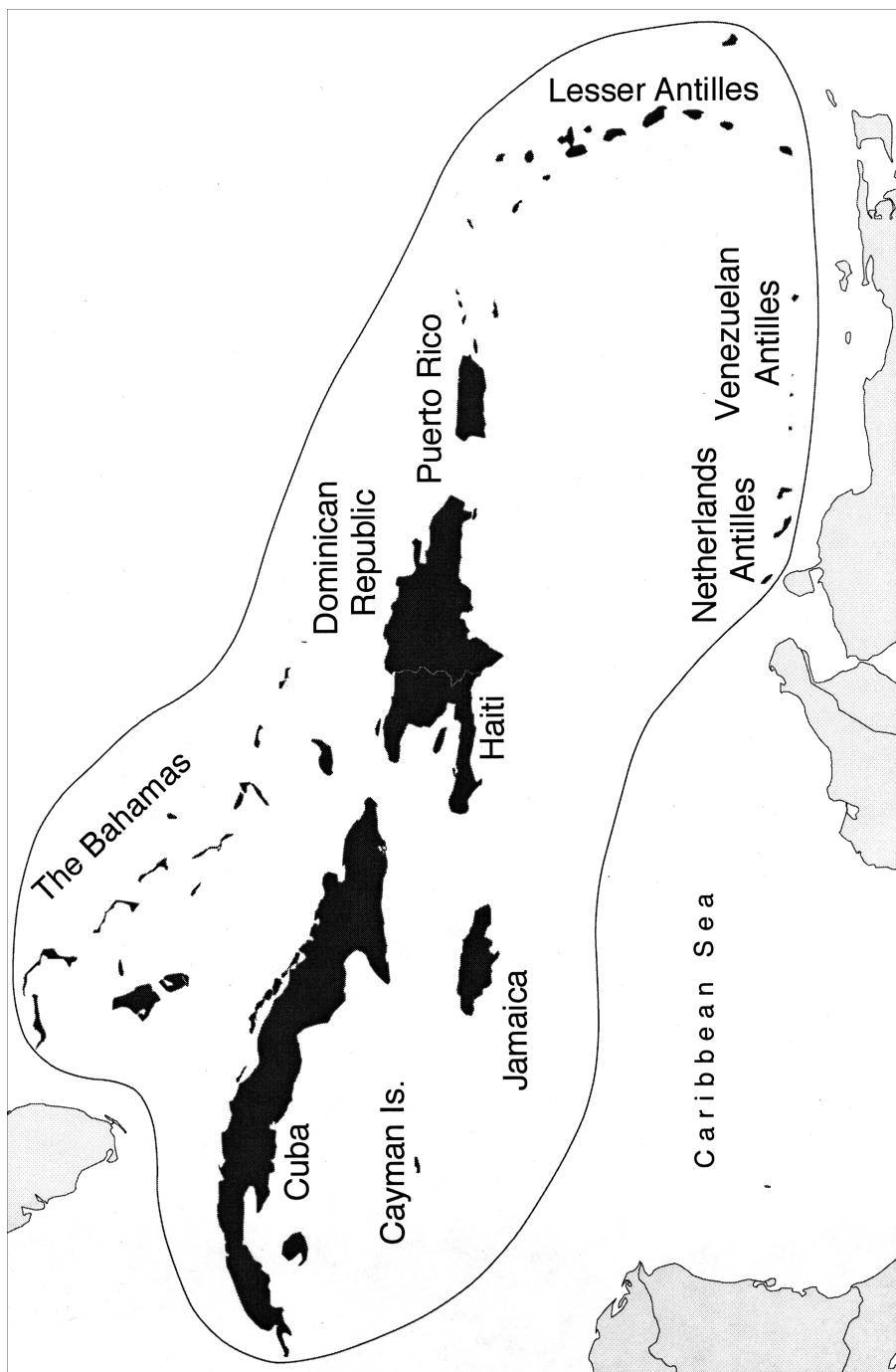


Fig. 1. The geographical distribution of the Caribbean Island Hotspot (Smith et al., 2004c).

patterns of plant endemism in the region. This initial approach will pave the way for future studies of other groups of endemic species. We provide a list of currently accepted endemic genera and compare the general patterns of generic diversity of this hotspot with those of other island systems worldwide. The term “endemic” is applied here strictly to taxa whose geographic ranges are totally confined or restricted to the islands of the hotspot (Fig. 1). Thus, Caribbean Island taxa with continental occurrence are excluded. In addition, we apply the term “indigenous taxa” to members of the flora of a particular region that have not been introduced by humans, including both “endemic” and “nonendemic” taxa.

Another objective of this paper is to discuss the phylogenetic placement of these endemic genera with reference to the latest phylogeny of seed plants (Soltis et al., 2005). We review the molecular phylogenies currently available for these genera and assess their utility and limitations for understanding the origin and evolutionary history of the Caribbean Island biota. This assessment will also identify priorities for future taxonomic/phylogenetic research.

#### PREVIOUS ACCOUNTS OF THE ENDEMIC GENERA

During the last 15 years, several books and research papers have reviewed biodiversity patterns for vertebrates and invertebrates endemic to the Caribbean Islands (e.g., Liebherr, 1988; Schwartz & Henderson, 1991; Smith et al., 1994; Hedges, 1996; Raffaele et al., 1998; Crother, 1999; Alberts, 2000; Dávalos, 2004). The extraordinary amount of information available on the fauna of the region contrasts with the relative paucity of information on plants. It is only in the last five years that comprehensive review papers on Antillean plants have been published (Graham, 2003a; Santiago-Valentín & Olmstead, 2004).

Two recent symposia on Antillean plants and on the status of molecular systematic research in Latin American countries have been important arenas of discussion and review of evolutionary and biogeographical patterns of plants found within the Caribbean Island Hotspot (Fritsch & McDowell, 2003; Francisco-Ortega, 2004; Michelangeli et al., 2004a). Our work aims to complement the information found in the research papers that resulted from these two symposia (Fritsch & McDowell, 2003; Francisco-Ortega, 2004).

A recent paper by Santiago-Valentín & Olmstead (2004) provided an updated review on the historical biogeography of Caribbean Island plants. This work compared plant diversity in the Caribbean with respect to seven other archipelagos of the world, and outlined major features of the geological history and paleovegetation of the islands. In addition, Santiago-Valentín & Olmstead (2004) reviewed several studies that used phylogenetic reconstructions to interpret the biogeography of this hotspot. The principal aim of their study was to summarize the contribution of different data sets to the development of historical biogeography hypotheses for Antillean plants. Our paper has a different approach; we focus on the endemic genera of the Caribbean Islands, and our paper is intended to be a tool for the development of conservation strategies in the region.

The endemic status or distribution of genera indigenous to the Antilles is found throughout the many contemporary floras of the region, published since 1946: the Bahamas (Correll & Correll, 1982); Cuba (León, 1946; León & Alain, 1951; Alain, 1953, 1957, 1962, 1969; Flora de la República de Cuba series, [www.bgbm.org/](http://www.bgbm.org/)); Cayman Is-

lands (Proctor, 1984); Hispaniola (Liogier, 1982, 1983, 1985a, 1986, 1989, 1994a, 1995a, 1995b, 1996, 2000); Jamaica (Adams, 1972); Lesser Antilles (Howard, 1974, 1979, 1988, 1989a, 1989b); Puerto Rico (Liogier, 1985b, 1988, 1994b, 1995b, 1997; Liogier & Martorell, 1982, 2000; Acevedo-Rodríguez & Strong, 2005); and Virgin Islands (Acevedo-Rodríguez, 1996).

Only two accounts, those by Howard (1973) and Borhidi (1991), focus on seed plant genera endemic to the Caribbean Islands as a whole. In these two studies, the information on these genera is scattered in numerous tables (28 tables in Howard's 1973 paper and 10 in Borhidi's 1991 paper), making the data difficult to handle. Because of their scope and objectives, these two compendia did not discuss the phylogenetic patterns of Antillean endemics, nor did they establish comparisons with other archipelagos worldwide. Howard's 1973 review, now more than three decades old, included most of the Caribbean Island Hotspot, while Borhidi's study (1991) did not include data from the Cayman Islands or Lesser Antilles.

### The Endemic Genera: Current Status, Historical Profile, and Comparisons with other Insular Hotspots

#### AN UPDATED LIST OF THE ENDEMIC GENERA

Data from the post-1946 floras of the Caribbean Islands, together with information from Howard's (1973) and Borhidi's (1991) accounts of the indigenous flora of the Antilles provided us an initial list of endemic genera for the region. This list was updated by consulting specialists in the taxonomy of specific groups and in floristics of the Antilles. We also consulted recent relevant monographs, taxonomic revisions, taxonomic checklists, and floras from the mainland and the Antilles (Table I). In addition, we conducted extensive searches in five major databases: Kew Bibliographic Database (Royal Botanic Gardens, Kew, 2005), Web of Science (Institute for Scientific Information, 2005), International Plant Names Index (International Plant Names Index, 2004), Index Nominum Genericum (Plantarum) (Farr & Zijlstra, 2005), and TROPICOS (Solomon, 2005). Additional information was retrieved from the Checklist of the West Indies (Acevedo-Rodríguez & Strong, in prep.).

We have identified a total of 180 endemic genera in 47 plant families (Table I). None of these endemic genera occur on Barbados nor on the eight island systems offshore of the Venezuelan coast (Aruba, Aves, Blanquilla, Bonaire, Curaçao, Orchilla, and Los Roques; Stoeffers, 1956; Gooding et al., 1965). Seventy-six of the genera considered endemic by Howard (1973) or Borhidi (1991), or in the floras of the region have been relegated to synonymy within other nonendemic genera (50 genera), or have recently been discovered on the mainland (26 genera) (Table II). Three additional genera, *Anilla*, *Proctoria*, and *Rondeletia*, have also been considered endemic in recent papers (Table II, Rova et al., 2002; McDowell et al., 2003; Luer, 2004). However, there is no agreement on their taxonomic rank or endemic status (Govaerts et al., 2006a; Ackerman, pers. comm.).

DNA phylogenies have been the basis for changing the endemic status of 10 of these genera (Table II) (i.e., *Belairia*, *Bembicidium*, *Calyptromoma*, *Corynella*, *Gastrococos*, *Margaritopsis*, *Notodon*, *Rajania*, *Sabinea*, and *Sauvallella*). They resolved as nested within other nonendemic or endemic genera.

Molecular data have also been important in the reinstatement of the endemic status

**Table I**

The 180 seed plant genera currently recognized as endemic to the Caribbean Islands. Approximate number of species recognized in each genus, insular distribution, and references supporting the endemic status of these genera are also indicated. Information on island distribution and approximate numbers of species was compiled from insular floras, references listed in this table, and other sources. Genera whose type species were first described in the endemic genus itself are indicated with an asterisk. Information on nomenclature, dates of publication, and types of endemic genera was obtained after consulting original descriptions and data compiled by Greuter et al. (1993) and Farr & Zijlstra (2005).

*Key:* B = Bahamas, C = Cuba, H = Hispaniola, J = Jamaica; L = Lesser Antilles, P = Puerto Rico, Y = Cayman Islands.

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
* <i>Acanthodesmos</i> C. D. Adams & duQuesnay, 1971	Asteraceae	1	J	Bremer, 1994
* <i>Achlaena</i> Griseb., 1866	Poaceae	1	C J	Filgueiras et al., 2001
* <i>Acidocroton</i> Griseb., 1859	Euphorbiaceae	10	C H J	Radcliffe-Smith, 2001
* <i>Acidoton</i> Sw., 1788	Euphorbiaceae	8	H J	Radcliffe-Smith, 2001
* <i>Acrosynanthus</i> Urb., 1913	Rubiaceae	7	C J	Govaerts et al., 2006a
<i>Acunaeanthus</i> Borhidi, Jarai-Komlódi & M. Moncada, 1981	Rubiaceae	1	C	Govaerts et al., 2006a
<i>Adenoa</i> Arbo, 1977	Turneraceae	1	C	Arbo, 1995
* <i>Anacaona</i> Alain, 1980	Cucurbitaceae	1	H	Jeffrey, 1990
<i>Ancistranthus</i> Lindau, 1900	Acanthaceae	1	C	Scotland & Vollesen, 2000
<i>Antillanorchis</i> Garay, 1974	Orchidaceae	1	C H	Nir, 2000
<i>Antillanthus</i> B. Nord., 2006	Asteraceae	17	C	Nordenstam, 2006a
<i>Antillia</i> R. M. King & H. Rob., 1971	Asteraceae	1	C	Bremer, 1994
* <i>Arcoa</i> Urb., 1923	Fabaceae	1	H	Lewis, 2005
* <i>Asciadium</i> Griseb., 1866	Apiaceae	1	C	Pimenov & Leonov, 1993
<i>Atopoglossum</i> Luer, 2004	Orchidaceae	3	C	Luer, 2004
<i>Auerodendron</i> Urb., 1924	Rhamnaceae	7	B C J P	Medan & Schirarend, 2004
<i>Barleriola</i> Oerst., 1854	Acanthaceae	5	C H P	Scotland & Vollesen, 2000
* <i>Behaimia</i> Griseb., 1859	Fabaceae	1	C	Schrire, 2005a
* <i>Bellonia</i> L., 1753	Gesneriaceae	2	C H	Weber, 2004
<i>Berylsimpsonia</i> B. L. Turner, 1993	Asteraceae	2	C H P	Turner, 1993
<i>Bisgoeppertia</i> Kuntze, 1891	Gentianaceae	2	C H	Thiv, 2002
* <i>Bonania</i> A. Rich., 1850	Euphorbiaceae	8	B C H	Radcliffe-Smith, 2001

**Table I** (*continued*)

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
* <i>Braasiella</i> Braem, Lückel & Rüssman, 1984	Orchidaceae	1	H	Nir, 2000
<i>Broughtonia</i> R. Br., 1813	Orchidaceae	6	B C H J P	Pridgeon et al., 2005
* <i>Brya</i> P. Browne, 1756	Fabaceae	4	C H J P	Klitgaard & Lavin, 2005
<i>Calycogonium</i> DC., 1828	Melastomataceae	36	C H J P	Judd, 1986
* <i>Caribeia</i> Alain, 1960	Nyctaginaceae	1	C	Bittrich & Kühn, 1993
<i>Ceratopyxis</i> Hook. f., 1872	Rubiaceae	1	C	Govaerts et al., 2006a
<i>Ceuthocarpus</i> Aiello, 1979	Rubiaceae	1	C	Govaerts et al., 2006a
<i>Charianthus</i> D. Don, 1823	Melastomataceae	6	L	Penneys & Judd, 2005
<i>Chascotheca</i> Urb., 1904	Phyllanthaceae	2	C H Y	Radcliffe-Smith, 2001; Govaerts, 2006
<i>Cheiophyllum</i> Britton, 1920	Scrophulariaceae	8	C J	Fischer, 2004
* <i>Ciceronia</i> Urb., 1925	Asteraceae	1	C	Bremer, 1994
<i>Coeloneurum</i> Radlk., 1889	Solanaceae	1	H	Santiago-Valentín & Olmstead, 2003
<i>Colleteria</i> David W. Taylor, 2003	Rubiaceae	2	C H P	Govaerts et al., 2006a
<i>Cubanola</i> Aiello, 1979	Rubiaceae	2	C H	Govaerts et al., 2006a
<i>Cubanthus</i> (Boiss.) Millsp., 1913	Euphorbiaceae	3	C H	Radcliffe-Smith, 2001
* <i>Dasytropis</i> Urb., 1924	Acanthaceae	1	C	Scotland & Vollesen, 2000
* <i>Dendrocousinsia</i> Millsp., 1913	Euphorbiaceae	3	J	Radcliffe-Smith, 2001
<i>Dendropemon</i> (Blume) Rchb., 1830	Loranthaceae	36	B C H J L P Y	Leiva, 1992; Acevedo-Rodríguez & Strong, in prep.
<i>Dilomilis</i> Raf., 1838	Orchidaceae	5	C H J P	Pridgeon et al., 2005
* <i>Ditta</i> Griseb., 1861	Euphorbiaceae	2	C H P	Radcliffe-Smith, 2001; Govaerts et al., 2006b
<i>Doerpfeldia</i> Urb., 1924	Rhamnaceae	1	C	Medan & Schirarend, 2004
<i>Domingoa</i> Schltr., 1913	Orchidaceae	3	C H P	Pridgeon et al., 2005; Govaerts et al., 2006c
<i>Ekmania</i> Gleason, 1919	Asteraceae	1	C	Bremer, 1994
<i>Ekmanianthe</i> Urb., 1924	Bignoniaceae	2	C H	Fischer et al., 2004
<i>Ekmaniopappus</i> Borhidi, 1992	Asteraceae	2	H	Borhidi et al., 1992
* <i>Ekmanochloa</i> Hitchc., 1936	Poaceae	2	C	Catasús-Guerra, 1997
<i>Elekmania</i> B. Nord., 2006	Asteraceae	9	H	Nordenstam, 2006a
<i>Encopella</i> Pennell, 1920	Scrophulariaceae	1	C	Fischer, 2004
* <i>Eosanthe</i> Urb., 1923	Rubiaceae	1	C	Govaerts et al., 2006a
* <i>Espadaea</i> A. Rich, 1850	Solanaceae	1	C	Santiago-Valentín & Olmstead, 2003

(continued)

**Table I** (*continued*)

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
* <i>Euchorium</i> Ekman Radlk., 1925	Sapindaceae	1	C	Acevedo-Rodríguez & Strong, in prep.
* <i>Euleria</i> Urb., 1925	Anacardiaceae	1	C	Mabberley, 1997
<i>Eupatorina</i> R. M. King & H. Rob., 1971	Asteraceae	1	H	Bremer, 1994
* <i>Feddea</i> Urb., 1925	Asteraceae	1	C	Bremer, 1994
* <i>Fuertesia</i> Urb., 1911	Loasaceae	1	H	Weigend, 2004
* <i>Fuertesiella</i> Schltr., 1913	Orchidaceae	1	CH	Pridgeon et al., 2003
* <i>Goetzea</i> Wydler, 1830	Solanaceae	2	H P	Santiago-Valentín & Olmstead, 2003
<i>Grimmeodendron</i> Urb., 1908	Euphorbiaceae	2	B C H J	Radcliffe-Smith, 2001
<i>Grisebachianthus</i> R. M. King & H. Rob., 1975	Asteraceae	8	C	Bremer, 1994
* <i>Gyrotaenia</i> Griseb., 1861	Urticaceae	4	C H J L	Friis, 1993
* <i>Haenianthus</i> Griseb., 1863	Oleaceae	2	C H J P	Zona, 1991
* <i>Haitia</i> Urb., 1919	Lythraceae	2	H	Graham, 2002
* <i>Harnackia</i> Urb., 1925	Asteraceae	1	C	Bremer, 1994
<i>Hebestigma</i> Urb., 1900	Fabaceae	1	C	Lavin & Schrire, 2005
<i>Hemithrinax</i> Hook. f., 1883	Arecaceae	3	C	Dransfield et al., 2005
<i>Henleophytum</i> H. Karst. 1861	Malpighiaceae	1	C	Anderson, 2003
* <i>Henoonia</i> Griseb., 1866	Solanaceae	1	C	Santiago-Valentín & Olmstead, 2003
* <i>Heptanthus</i> Griseb., 1866	Asteraceae	7	C	Bremer, 1994
* <i>Herodotia</i> Urb. & Ekman, 1926	Asteraceae	1	H	Bremer, 1994
<i>Herpyza</i> C. Wright, 1869	Fabaceae	1	C	Schrire, 2005b
<i>Herrananthus</i> B. Nord., 2006	Asteraceae	1	C	Nordenstam, 2006a
* <i>Hottea</i> Urb., 1929	Myrtaceae	7	C H	Borhidi, 1992
<i>Ignurbia</i> B. Nord., 2006	Asteraceae	1	H	Nordenstam, 2006b
<i>Isidorea</i> DC., 1830	Rubiaceae	17	C H	Govaerts et al., 2006a
* <i>Kodalyodendron</i> Borhidi & Acuna, 1973	Rutaceae	1	C	Borhidi et al., 1973
* <i>Koehneola</i> Urb., 1901	Asteraceae	1	C	Bremer, 1994
* <i>Lachnorhiza</i> A. Rich., 1850	Asteraceae	2	C	Bremer, 1994
* <i>Lagetta</i> Juss., 1789	Thymelaeaceae	4	C H J	Herber, 2003; Acevedo-Rodríguez & Strong, in prep.
* <i>Lantanopsis</i> Griseb., 1862	Asteraceae	3	C H	Bremer, 1994
<i>Lasiocroton</i> Griseb., 1859	Euphorbiaceae	5	B C H J	Radcliffe-Smith, 2001; Jestrow et al., in prep.
<i>Leonis</i> B. Nord., 2006	Asteraceae	1	C H	Nordenstam, 2006a
<i>Leptocereus</i> (A. Berger) Britton & Rose, 1909	Cactaceae	12	C H P Y	Barthlott & Hunt, 1993
* <i>Leptogonium</i> Benth., 1880	Polygonaceae	1	H	Brandbyge, 1993
* <i>Lepturidium</i> Hitchc. & Ekman, 1936	Poaceae	1	C	Catasús-Guerra, 1997
* <i>Lescaillea</i> Griseb., 1866	Asteraceae	2	C	Bremer, 1994
* <i>Leucocroton</i> Griseb., 1861	Euphorbiaceae	28	C H	Radcliffe-Smith, 2001
* <i>Linodendron</i> Griseb., 1861	Thymelaeaceae	4	C	Herber, 2003
<i>Lucya</i> DC., 1830	Rubiaceae	1	C H J P	Govaerts et al., 2006a
<i>Lundinia</i> B. Nord., 2006	Asteraceae	1	C H	Nordenstam, 2006a

**Table I** (*continued*)

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
* <i>Mattfeldia</i> Urb., 1931	Asteraceae	1	H	Bremer, 1994
<i>Mazaea</i> Krug & Urb., 1897	Rubiaceae	2	C	Govaerts et al., 2006a
<i>Mecranium</i> Hook f., 1867	Melastomataceae	23	C H J P	Skean, 1993
<i>Micrasepalum</i> Urb., 1913	Rubiaceae	2	C H	Govaerts et al., 2006a
<i>Microcycas</i> (Miq.) A. DC., 1868	Zamiaceae	1	C	Stevenson, 1992
<i>Mniochloa</i> Chase, 1908	Poaceae	1	C	Catasús-Guerra, 1997
* <i>Moacroton</i> Croizat, 1945	Euphorbiaceae	8	C	Radcliffe-Smith, 2001
* <i>Nashia</i> Millsp., 1906	Verbenaceae	7	B C H P	Atkins, 2004
<i>Neobracea</i> Britton, 1920	Apocynaceae	8	B C	Endress & Bruyns, 2000
* <i>Neobuchia</i> Urb., 1902	Malvaceae	1	H	Bayer & Kubitzki, 2003
<i>Neocogniauxia</i> Schltr., 1913	Orchidaceae	2	H J	Pridgeon et al., 2005
<i>Neomezia</i> Votsch, 1904	Theophrastaceae	1	C	Ståhl, 2004
* <i>Neoregnellia</i> Urb., 1924	Malvaceae	1	C H	Bayer & Kubitzki, 2003
<i>Neorudolphia</i> Britton, 1924	Fabaceae	1	P	Schrire, 2005b
<i>Nesampelos</i> B. Nord., 2006	Asteraceae	3	H	Nordenstam, 2006a
<i>Nodocarpaea</i> A. Gray, 1883	Rubiaceae	1	C	Govaerts et al., 2006a
<i>Odontocline</i> B. Nord., 1978	Asteraceae	6	J	Bremer, 1994
<i>Oldfelta</i> B. Nord. & Lundin, 2002	Asteraceae	1	C	Nordenstam & Lunden, 2002
<i>Osmiopsis</i> R. M. King & H. Rob. 1975	Asteraceae	1	H	Bremer, 1994
* <i>Ottoschmidia</i> Urb., 1924	Rubiaceae	1	C H	Govaerts et al., 2006a
* <i>Pedinopetalum</i> Urb. & H. Wolff, 1929	Apiaceae	1	H	Pimenov & Leonov, 1993
<i>Penelopeia</i> Urb., 1921	Cucurbitaceae	1	H	Jeffrey, 1990
* <i>Petitia</i> Jacq., 1760	Lamiaceae	2	B C H J P Y	Harley et al., 2004
* <i>Phania</i> DC., 1836	Asteraceae	5	C H	Bremer, 1994
<i>Phedonocarpa</i> L. E. Skog, 1976	Gesneriaceae	1	C J	Weber, 2004
* <i>Phialanthus</i> Griseb., 1861	Rubiaceae	18	B C H J P	Motley et al., 2005
* <i>Phlebotaea</i> Griseb., 1861	Polygonaceae	2	C P	Rankin-Rodríguez, 2003
<i>Phyllacanthus</i> Hook. f., 1871	Rubiaceae	1	C	Govaerts et al., 2006a
* <i>Phyllohelia</i> Griseb., 1866	Rubiaceae	1	C	Govaerts et al., 2006a
* <i>Picardaea</i> Urb., 1903	Rubiaceae	1	C H	Govaerts et al., 2006a
<i>Picrodendron</i> Griseb., 1860	Picrodendracea	1	B C H J Y	Radcliffe-Smith, 2001
* <i>Pictetia</i> DC., 1825	Fabaceae	8	C H P	Klitgaard & Lavin, 2005
<i>Pinillosia</i> Ossa, 1836	Asteraceae	1	C H	Bremer, 1994
<i>Piresiella</i> Judzie., Zulo. & Morr., 1993	Poaceae	1	C	Catasús-Guerra, 1997
* <i>Platygyne</i> Mercier, 1830	Euphorbiaceae	7	C	Radcliffe-Smith, 2001
<i>Plethadenia</i> Urb., 1912	Rutaceae	2	C H	Beurton, 2000
* <i>Poitea</i> Vent., 1807	Fabaceae	12	C H L P	Lavin & Schrire, 2005
* <i>Portlandia</i> P. Browne, 1756	Rubiaceae	7	J	Motley et al., 2005
* <i>Priamosia</i> Urb., 1919	Flacourtiaceae	1	H	Sleumer, 1980
<i>Pseudocarpidium</i> Millsp., 1906	Lamiaceae	8	B C H	Harley et al., 2004
<i>Psychilis</i> Raf., 1836	Orchidaceae	15	H L P	Pridgeon et al., 2005
* <i>Quisqueya</i> Dod, 1979	Orchidaceae	4	H	Pridgeon et al., 2005
<i>Reynaudia</i> Kunth, 1830	Poaceae	1	C H J	Catasús-Guerra, 2002
* <i>Rhodogerion</i> Griseb., 1866	Asteraceae	1	C	Anderberg et al., 2005

(continued)

**Table I** (*continued*)

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
<i>Rhodopis</i> Urb., 1900	Fabaceae	2	H	Schrire, 2005b
<i>Roigella</i> Borhidi & M. Fernández Zeq., 1981	Rubiaceae	1	C	Govaerts et al., 2006a
* <i>Salcedoa</i> F. Jiménez R. & L. Katinas, 2004	Asteraceae	1	H	Jiménez-Rodríguez et al., 2004
* <i>Salpixantha</i> Hook., 1845	Acanthaceae	1	J	Profice, 2002
* <i>Samuelssonia</i> Urb. & Ekman, 1929	Acanthaceae	1	H	Scotland & Vollesen, 2000
* <i>Sapphoa</i> Urb., 1922	Acanthaceae	2	C	Borhidi, 1983
* <i>Sarcopilea</i> Urb., 1912	Urticaceae	1	H	Friis, 1993
* <i>Saugetia</i> Hitch. & Chase, 1917	Poaceae	2	C H	Catasús-Guerra, 1997
* <i>Sauvallea</i> W. Wright, 1871	Commelinaceae	1	C	Faden, 1998
* <i>Schmidtottia</i> Urb., 1923	Rubiaceae	16	C	Motley et al., 2005
<i>Scolosanthus</i> Vahl, 1796	Rubiaceae	20	B C H J P	Govaerts et al., 2006a; Acevedo-Rodríguez & Strong, in prep.
<i>Scutachne</i> Hitch. & Chase, 1911	Poaceae	2	C H J	Catasús-Guerra, 1997
* <i>Selleophyllum</i> Urb., 1915	Asteraceae	1	H	Kimball & Crawford, 2004
* <i>Seymeriopsis</i> Tsevelev, 1987	Scrophulariaceae	1	C	Fischer, 2004
* <i>Shafera</i> Greenm., 1912	Asteraceae	1	C	Bremer, 1994
* <i>Shaférocharis</i> Urb., 1912	Rubiaceae	3	C	Govaerts et al., 2006a
<i>Siemensia</i> Urb., 1923	Rubiaceae	1	C	Govaerts et al., 2006a
* <i>Solonia</i> Urb., 1922	Myrsinaceae	1	C	Panfet-Valdés, 2005
* <i>Spaniopappus</i> B. L. Rob., 1926	Asteraceae	5	C	Bremer, 1994
<i>Spirotecoma</i> Dalla Torre & Harms, 1904	Bignoniaceae	7	C H	Fischer et al., 2004
* <i>Stahlia</i> Bello, 1881	Fabaceae	1	H P	Lewis, 2005
* <i>Stevensia</i> Poit., 1804	Rubiaceae	11	H	Govaerts et al., 2006a
<i>Strempeliopsis</i> Benth., 1876	Apocynaceae	2	C J	Endress & Bruyns, 2000
<i>Suberanthus</i> Borhidi & M. Fernández Zeq., 1981	Rubiaceae	7	C H	Govaerts et al., 2006a
* <i>Synapsis</i> Griseb., 1866	Scrophulariaceae	1	C	Fischer, 2004
* <i>Tétralix</i> Griseb., 1866	Malvaceae	5	C	Bayer & Kubitzki, 2003
<i>Tetramicra</i> Lindley, 1831	Orchidaceae	13	B C H J L P	Pridgeon et al., 2005
* <i>Tetranthus</i> Sw., 1788	Asteraceae	4	B H	Bremer, 1994
<i>Tetraperone</i> Urb., 1901	Asteraceae	1	C	Bremer, 1994
* <i>Tetrasiphon</i> Urb., 1904	Celastraceae	1	J	Simmons, 2004
* <i>Theophrasta</i> L., 1753	Theophrastaceae	2	H	Ståhl, 2004
<i>Thogsennia</i> Aiello, 1979	Rubiaceae	1	C H	Govaerts et al., 2006a
<i>Thymopsis</i> Benth., 1873	Asteraceae	2	B C	Bremer, 1994

**Table I** (*continued*)

Genus <sup>a</sup> and date of its description	Family	n	Distribution <sup>b</sup>	Reference
<i>Tomzanonia</i> Nir, 1997	Orchidaceae	1	H	Pridgeon et al., 2005
<i>Torralbasia</i> Krug & Urb., 1900	Celastraceae	1	C H P	Simmons, 2004
* <i>Tortuella</i> Urb., 1927	Rubiaceae	1	H	Govaerts et al., 2006a
* <i>Triscenia</i> Griseb., 1862	Poaceae	1	C	Catasús-Guerra, 1997
<i>Urbananthus</i> R. M. King & H. Rob., 1971	Asteraceae	2	C J	Bremer, 1994
* <i>Vegaea</i> Urb., 1913	Myrsinaceae	1	H	Ståhl & Anderberg, 2004
* <i>Verhuellia</i> Miq., 1843	Piperaceae	2	C H	Wanke et al., 2006
<i>Wallenia</i> Sw., 1788	Myrsinaceae	40	B C H J L P	Panfet-Valdés, 2005
* <i>Woehleria</i> Griseb., 1861	Amaranthaceae	1	C	Townsend, 1993
<i>Zemisia</i> B. Nord., 2006	Asteraceae	1	J	Nordenstam, 2006a
<i>Zombia</i> L. H. Bailey, 1939	Arecaceae	1	H	Uhl & Dransfield, 1987
* <i>Zonanthus</i> Griseb., 1862	Gentianaceae	1	C	Thiv, 2002

<sup>a</sup> *Antilla* Luer (12 spp.) and *Proctoria* Luer (unispecific) are recently described genera considered endemic to the Antilles by Luer (2004); additional studies are needed to confirm the taxonomic status of these taxa. Molecular data from Rova et al. (2002) suggest that *Rondeletia* L. might represent another genus endemic to the Antilles. McDowell et al. (2003) follow this view. In its broadest sense, this is a large genus (~250 spp.), and we believe that additional data are needed to understand its taxonomy (i.e., Govaerts et al., 2006a).

<sup>b</sup> Govaerts et al. (2006a) reported *Phialanthus* in Florida. However, this genus does not occur there (Wunderlein & Hansen, 2003; 2004). Govaerts et al. (2006a) also indicated *Rhachicallis* DC. (Rubiaceae) as endemic to the Antilles; however, this genus is also known to occur in Mesoamerica (Lorence, 1999).

of at least one Antillean genus. *Selleophyllum*, a Haitian taxon originally described by Urban (1915), was considered by Sherff and Alexander (1955) to belong to *Coreopsis* L. However, a recent molecular phylogeny developed by Kimball and Crawford (2004) demonstrates that it should be recognized as a distinct genus, as suggested by Urban (1915). In addition, phylogenetic reconstructions based on morphological traits have been useful for assigning a generic status to *Salcedoa*, one of the most recently described endemic genera (Jiménez-Rodríguez et al., 2004).

Taxonomic ranks, particularly above species level, are traditionally subjective. For many systematists, the only requirement for assigning ranks is that the target group must be monophyletic (Judd et al., 1999). In addition, generic concepts vary among plant taxonomists, and are usually influenced by the taxonomic history and tradition of each particular family (Davis & Heywood, 1963; Stace, 1980; Bramwell, 1983; Stuessy, 1990). In spite of these limitations, we believe that our study reflects a comprehensive review and that the accepted genera reflect the current opinion of taxonomic experts. Nevertheless, many of these genera have not been the subject of phylogenetic studies; thus, their taxonomic status and monophyly are still uncertain. In addition, we are aware that several unique Antillean radiations of large genera such as *Miconia* Ruiz & Pav. (Melastomataceae) or *Croton* L. (Euphorbiaceae) are poorly understood. Species in these groups might be assigned to other genera once additional systematic studies are available. This has been the case for endemic species previously accommodated in the

**Table II**

The 76 seed plant genera considered endemic to the Antilles by León (1946), León and Alain (1951), Alain (1953, 1957, 1960, 1962, 1969), Liogier (1982, 1983, 1985a, 1985b, 1986, 1988, 1989, 1994a, 1994b, 1995a, 1995b, 1996, 1997, 2000), Howard (1973), Correll & Correll (1982), or Borhidi (1991) that currently are not regarded as endemic to this region

Genus	Family	Synonymy or distribution outside Antilles	Reference
<i>Adenopores</i> J. K. Small	Malpighiaceae	= <i>Tetrapterys</i> Cav.	Anderson, 2003
<i>Ampelocera</i> Klotsch	Ulmaceae	South & Central America	Todzia, 1989
<i>Amphiolanthus</i> Griseb.	Scrophulariaceae	= <i>Micranthemum</i> Michx.	Fischer, 2004
<i>Ancistrophora</i> A. Gray	Asteraceae	= <i>Verbesina</i> L.	Olsen, 1986
<i>Anthacanthus</i> Nees	Acanthaceae	= <i>Oplonia</i> Raf.	Stearn, 1971
<i>Ariadne</i> Urb.	Rubiaceae	= <i>Mazaea</i> Krug & Urb.	Govaerts et al., 2006a
<i>Atkinsia</i> R. A. Howard	Malvaceae	= <i>Thespesia</i> Corrêa	Fryxell, 1988
<i>Belairia</i> A. Rich.	Fabaceae	= <i>Pictetia</i> DC.	Klitgaard & Lavin, 2005
<i>Bembicidium</i> Rydb.	Fabaceae	= <i>Poitea</i> Vent.	Lavin & Schrire, 2005
<i>Calyptronoma</i> Griseb.	Arecaceae	= <i>Calyptrogyne</i> H. Wendl.	Roncal et al., 2005a; 2005b
<i>Cameraria</i> L.	Apocynaceae	Neotropical	Mabberley, 1997
<i>Casabitoa</i> Alain	Picramniaceae	= <i>Picramnia</i> Sw.	Zanoni & García, 1994
<i>Cattleyopsis</i> Lem.	Orchidaceae	= <i>Broughtonia</i> R. Br.	Nir, 2000
<i>Chaetium</i> Nees	Poaceae	Mexico to Brazil	Clayton & Renvoize, 1986
<i>Chaetocarpus</i> Thwaites	Euphorbiaceae	Tropical Africa, Asia & New World	Radcliffe-Smith, 2001
<i>Cionosicyos</i> Griseb.	Cucurbitaceae	Central America	Jeffrey, 2001
<i>Colpothrinax</i> Griseb. & H. Wendl.	Arecaceae	Central America	Evans, 2001
<i>Corynella</i> DC.	Fabaceae	= <i>Poitea</i> Vent.	Lavin & Schrire, 2005
<i>Cryptorhiza</i> Urb.	Myrtaceae	= <i>Pimenta</i> Lindl.	Landrum, 1986
<i>Cubacroton</i> Alain	Euphorbiaceae	= <i>Moacroton</i> Croizat	Radcliffe-Smith, 2001
<i>Cybianthopsis</i> (Mez) Lundell	Myrsinaceae	= <i>Cybianthus</i> Mart.	Agostini, 1980
<i>Davilla</i> Vand.	Dilleniaceae	Neotropical	Pérez-Camacho & Cejas-Rodríguez, 1993
<i>Dendrocereus</i> Britton & Rose	Cactaceae	= <i>Acanthocereus</i> (A. Berger) Britton & Rose	Barthlott & Hunt, 1993
<i>Dinema</i> Lindl.	Orchidaceae	Neotropical	Nir, 2000
<i>Distictis</i> Meisn.	Bignoniaceae	South, Central & North America	Fischer et al., 2004
<i>Ekmaniocharis</i> Urb.	Melastomataceae	= <i>Mecranium</i> Hook f.	Skean, 1993
<i>Gastrococos</i> Morales	Arecaceae	= <i>Acrocomia</i> Mart.	Gunn, 2004
<i>Gaussia</i> H. Wendl.	Arecaceae	North America	Uhl & Dransfield, 1987

**Table II** (*continued*)

Genus	Family	Synonymy or distribution outside Antilles	Reference
<i>Goerziella</i> Urb.	Amaranthaceae	= <i>Amaranthus</i> L.	Mosyakin & Robertson, 1996
<i>Gundlachia</i> A. Gray	Asteraceae	North & South America	Urbatsch & Roberts, 2004
<i>Homalopetalum</i> Rolfe	Orchidaceae	Neotropical	Nir, 2000
<i>Hybosperma</i> Urb.	Rhamnaceae	= <i>Colubrina</i> Brongn.	Medan & Schirarend, 2004
<i>Jacaima</i> Rendle	Apocynaceae	= <i>Matelea</i> Aubl.	Morillo, 1986
<i>Jacmaia</i> B. Nord.	Asteraceae	Costa Rica	Bremer, 1994
<i>Krokia</i> Urb.	Myrtaceae	= <i>Pimenta</i> Lindl	Landrum, 1986
<i>Laeliopsis</i> Lindl. & Paxton	Orchidaceae	= <i>Broughtonia</i> R. Br.	Nir, 2000
<i>Macrocarpaea</i> (Griseb.) Gilg	Gentianaceae	Central & South America	Struwe et al., 2002
<i>Manekia</i> Trel.	Piperaceae	= <i>Sarcorhachis</i> Trel.	Bornstein, 1996
<i>Margaritopsis</i> C. Wright	Rubiaceae	Pantropical	Andersson, 2001
<i>Megalopanax</i> Ekman	Araliaceae	= <i>Aralia</i> L.	Wen, 1993
<i>Mettenia</i> Griseb.	Euphorbiaceae	= <i>Chaetocarpus</i> Thwaites	Radcliffe-Smith, 2001
<i>Mommsenia</i> Urb. & Ekman	Melastomataceae	= <i>Calycogonium</i> DC.	Judd & Skean, 1991
<i>Mozartia</i> Urb.	Myrtaceae	= <i>Myrcia</i> Guill.	Liogier, 1971
<i>Myrtekmania</i> Urb.	Myrtaceae	= <i>Pimenta</i> Lindl	Landrum, 1986
<i>Narvalina</i> Cass.	Asteraceae	South America	Bremer, 1994
<i>Neoabbottia</i> Britton & Rose	Cactaceae	= <i>Leptocereus</i> (A. Berger) Britton & Rose	Barthlott & Hunt, 1993
<i>Neolaugeria</i> Nicolson	Rubiaceae	= <i>Stenostomum</i> C. F. Gaetn.	Govaerts et al., 2006a
<i>Neomazaea</i> Krug & Urb.	Rubiaceae	= <i>Mazaea</i> Krug & Urb.	Govaerts et al., 2006a
<i>Neothymopsis</i> Britton & Millsp.	Asteraceae	= <i>Thymopsis</i> Benth.	Alain, 1960
<i>Neo-urbania</i> Faw. & Rendle	Orchidaceae	= <i>Maxillaria</i> Ruiz & Pav.	Nir, 2000
<i>Notodon</i> Urb.	Fabaceae	= <i>Poitea</i> Vent.	Lavin & Schrire, 2005
<i>Ottoschulzia</i> Urb.	Icacinaceae	Central America	Lundell, 1975
<i>Peltostigma</i> Walp.	Rutaceae	North, Central & South America	Jiménez & Gereau, 1991
<i>Peratanthe</i> Urb.	Rubiaceae	= <i>Coprosma</i> J. R. Forst. & G. Forst.	Govaerts et al., 2006a
<i>Phidiasia</i> Urb.	Acanthaceae	= <i>Odontonema</i> Nees	Mabberley, 1997
<i>Pinosia</i> Urb.	Caryophyllaceae	= <i>Drymaria</i> Schult.	Duke, 1961
<i>Piperanthera</i> C. DC.	Piperaceae	= <i>Peperomia</i> Ruiz & Pav.	Mabberley, 1997
<i>Piptocoma</i> Cass.	Asteraceae	Central & South America	Pruski, 1996
<i>Pleodendron</i> Tiegh.	Canellaceae	Central America	Hammel & Zamora, 2005
<i>Pterocissus</i> Urb. & Ekman	Vitaceae	= <i>Cissus</i> L.	Lombardi, 1997
<i>Rajania</i> L.	Dioscoreaceae	= <i>Dioscorea</i> L.	Raz, in prep.
<i>Rhytidophyllum</i> Mart.	Gesneriaceae	South America	Skog, 1976
<i>Rousselia</i> Gaudich.	Urticaceae	Central & South America	Friis, 1993
<i>Sabinea</i> DC.	Fabaceae	= <i>Poitea</i> Vent.	Lavin & Schrire, 2005
<i>Sarcomphalus</i> P. Browne	Rhamnaceae	= <i>Ziziphus</i> Mill.	Johnston, 1964

(continued)

**Table II** (*continued*)

Genus	Family	Synonymy or distribution outside Antilles	Reference
<i>Sauvallrella</i> Rydb.	Fabaceae	= <i>Poitea</i> Vent.	Lavin & Schrire, 2005
<i>Savia</i> Willd.	Euphorbiaceae	Neotropics, East & South Africa, Madagascar	Radcliffe-Smith, 2001
<i>Selleola</i> Urb.	Caryophyllaceae	= <i>Minuartia</i> L.	Bittrich, 1993
<i>Spathelia</i> L.	Rutaceae	South America	Gentry, 1992
<i>Terebraria</i> Kuntze	Rubiaceae	= <i>Stenostemum</i> C. F. Gaetn.	Govaerts et al., 2006a
<i>Triopterys</i> L.	Malpighiaceae	Neotropical	Mabberley, 1997
<i>Ulbrichtia</i> Urb.	Malvaceae	= <i>Thespesia</i> Corrêa	Fryxell, 1988
<i>Victorinia</i> León	Euphorbiaceae	= <i>Cnidoscolus</i> Pohl	Radcliffe-Smith, 2001
<i>Websteria</i> S. H. Wright	Cyperaceae	Tropics and subtropics	Goetghebeur, 1998
<i>Wunschmannia</i> Urb.	Bignoniaceae	= <i>Distictis</i> Meisn.	Fischer et al., 2004
<i>Ximeniopsis</i> Alain	Olacaceae	= <i>Ximenia</i> L.	Sleumer, 1984

large genera *Eupatorium* L. and *Senecio* L. (Asteraceae). Many of the *Eupatorium* species are currently placed in five endemic genera (King & Robinson, 1987), whereas those in *Senecio* are in 10 endemic genera (Nordenstam, 1978, 2006a, 2006b; Nordenstam & Lunden, 2002).

The five families with the highest number of Caribbean Island endemic genera are Asteraceae (39), Rubiaceae (27), Orchidaceae (12), Euphorbiaceae (11), and Fabaceae (10). These five families are also among the seven most generically diverse (>100 genera) in the New World (the others being the Melastomataceae and Poaceae). Therefore, at the family level, patterns of generic endemism in the Hotspot appear congruent with those of tropical regions of the New World (Smith et al., 2004d; Table I). However, it is noteworthy that at least three families (i.e., Araceae, Cyperaceae, and Lauraceae) that have a high number of genera restricted to the neotropics do not have any genera endemic to the Caribbean Islands (Goetghebeur, 1998; Croat, 2004; Madriñán, 2004). Likewise, the Arecaceae, a family with at least 60 neotropical endemic genera, have only two genera restricted to the Antilles, *Hemithrinax* and *Zombia* (Dransfield et al., 2005; Zona et al., in press). Only one of the 25 families endemic to the neotropics, Theophrastaceae, is represented in our updated list by two endemic genera, *Neomezia* and *Theophrasta* (Ståhl, 2004). The highly threatened Cuban *Microcycas* is the only endemic gymnosperm genus within the Caribbean Island Hotspot (Stevenson, 1992).

The 180 endemic Caribbean Island genera comprise approximately 727 species (Tables I and III); this is a relatively small portion of the plant species endemic to the region. While efforts are underway to produce a checklist (Acevedo-Rodríguez & Strong, in prep.) and a Red List of Antillean plants, we do not as yet have authoritative data on all endemic/indigenous species. This precludes our understanding of the impact that the endemic genera have on the overall species richness of the Caribbean Island Hotspot.

On the basis of several sources, Santiago-Valentín & Olmstead (2004) estimated that the Antilles have approximately 1289 indigenous genera and 8000 endemic species of vascular plants. Although these are imprecise values, we have used them as a baseline

**Table III**  
Taxonomic biodiversity of the Caribbean Islands and 19 additional islands/archipelagos

Island or archipelago	Number of endemic genera/unispecific endemic genera	Number of indigenous genera <sup>c</sup>	Number of species in endemic genera	Number of endemic species	Number of indigenous species <sup>c</sup>	Reference
Canaries	22/13	731	43	570	1300	Santos-Guerra, 2001
Cape Verde	1/0	72	5	65	274	Brochmann et al., 1997;
Caribbean Islands	180/92	1289 <sup>a</sup>	727	8000 <sup>a</sup>	12,000 <sup>a</sup>	Arechavala et al., 2005
Crete	2/2	623	2	158	1699	Santiago-Valentín & Olmstead, 2004
Fiji	12/9	478	16	812	1318	Barclay, 1986; Fielding & Turland, 2005
Galapagos	7/4	309	23	216	487	Wiggins & Porter, 1971; McMullen, 1999
Hawaiian	32/6	956	278	850	956	Wagner et al., 1990; Carr, 2005
Japan	22/16	999	24	1449	3834	Shimizu, 1988
Juan Fernández	11/6	80	30	103	158	Stuessy et al., 1992
Madagascar	260(?) <sup>b</sup>	1289(?) <sup>b</sup>	?	8000 <sup>b</sup>	10,000 <sup>b</sup>	Strahm, 1994
Maderia-Selvagens	4/3	319	5	116	1156	Press & Short, 2001
Malesian Islands: <sup>d</sup>						
Borneo	62/39	?	112	6000 <sup>a</sup>	25,000 <sup>a</sup>	Davis, 1995; Wong, 1998
New Guinea	84/56	1465	189	16,000	20,000	Davis, 1995; Johns, 1995b; Damas, 1998
Philippines	24/18	?	41	3500 <sup>a</sup>	8900 <sup>a</sup>	Davis, 1995; Johns, 1995b
Sulawesi	8/7	?	9	?	5000 <sup>a</sup>	Davis, 1995; Johns, 1995b
Sumatra	10/9	?	11	>1200 <sup>a</sup>	>10,000 <sup>a</sup>	Davis, 1995; Johns, 1995b
Marquesas	2/2	124	2	115	210	Wagner, 1990
New Caledonia	10/446	763	391	2478	3137	Lowry, 1998; Jaffré et al., 2004
New Zealand	49/28	361	105	1566	1896	Wilton & Breitwieser, 2000

(continued)

**Table III** (*continued*)

Island or archipelago	Number of endemic genera/unispecific endemic genera <sup>a</sup>	Number of indigenous genera <sup>c</sup>	Number of species in endemic genera	Number of endemic species	Number of indigenous species <sup>c</sup>	Reference
Seychelles	12/11	179	13	69	222	Procter, 1984; Wise, 1998
St. Helena	10/7	38	15	36	290	Cronk, 2000; Brown, 1982
Society	2/2	214	2	192	414	Welsh, 1998
Socotra	15/12	411	19	306	798	Miller & Morris, 2004;
Taiwan	4/4	1419	4	995	3448	Miller, pers. comm. Hsich, 2003

<sup>a</sup> Values for all vascular plants.<sup>b</sup> Values for flowering plants only.<sup>c</sup> Number of indigenous taxa include both endemic and nonendemic components of flora, excluding species introduced because human activities.<sup>d</sup> Data for single-island endemic genera only.

**Table IV**

Endemicity percentages at generic level for the Caribbean Islands and 19 additional islands/archipelagos. Percentages are derived from data shown in Table III

Island systems	Percentage of endemic genera reported as unispecific	Percentage of indigenous genera reported as endemic <sup>a</sup>	Percentage of endemic species found within the endemic genera
Canaries	59	3	7
Cape Verde	0	1	8
Caribbean Islands	51	14	9
Crete	100	<1	1
Fiji	75	3	2
Galapagos	57	2	11
Hawaiian	19	3	32
Japan	73	2	2
Juan Fernández	54	14	29
Madagascar	?	20	?
Madeira-Selvagens	75	1	4
Malesian Islands: <sup>b</sup>			
Borneo	63	55	2
New Guinea	67	6	1
Philippines	75	?	1
Sulawesi	87	?	?
Sumatra	90	?	<1
Marquesas	100	2	2
New Caledonia	44	14	16
New Zealand	57	13	7
Seychelles	92	15	19
St. Helena	70	26	42
Society	100	1	1
Socotra	80	3	5
Taiwan	100	<1	<1

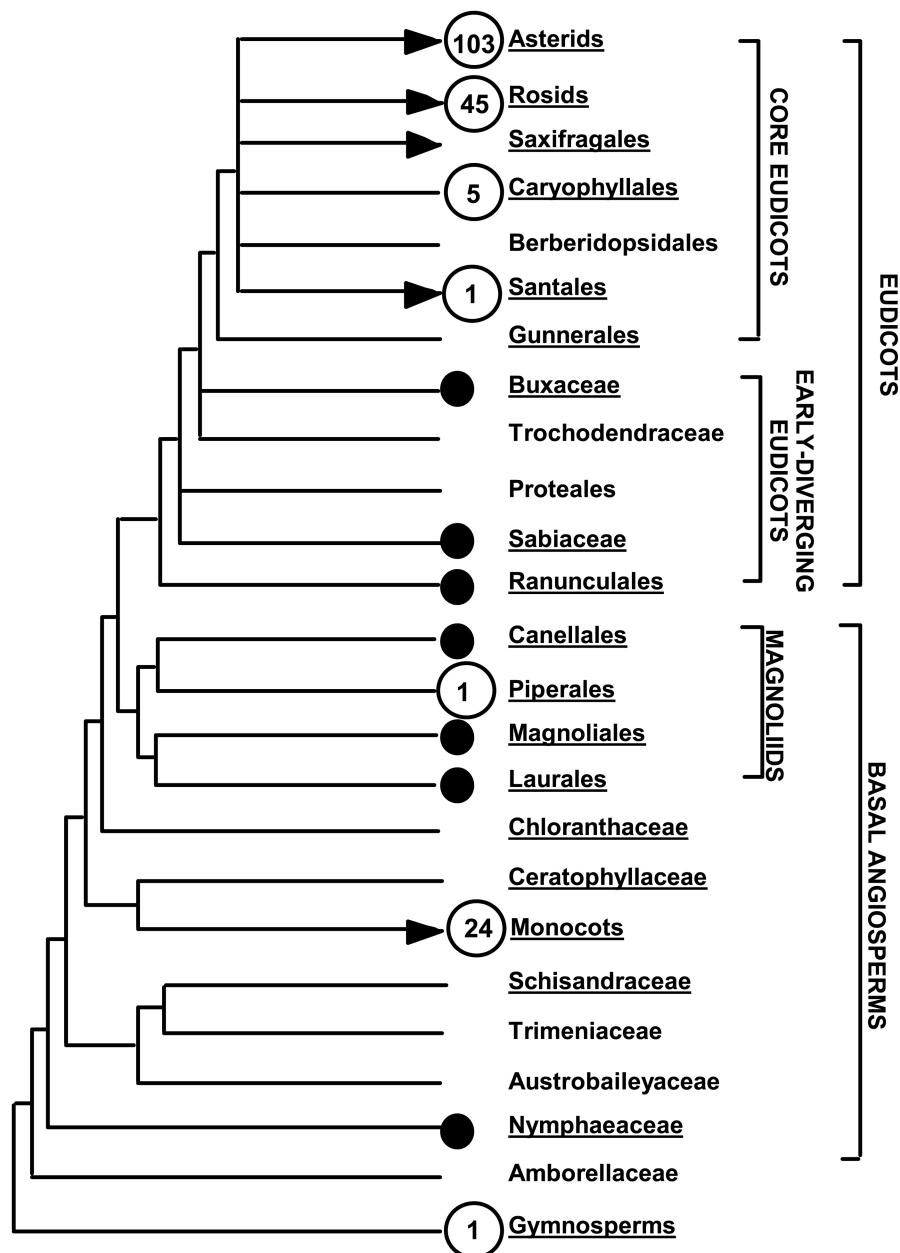
<sup>a</sup> Number of indigenous taxa include both endemic and nonendemic components of flora, excluding species introduced because human activities.

<sup>b</sup> Data for single-island endemic genera only.

reference to calculate conservative percentages of taxonomic diversity within the endemic genera. The 727 species found in the endemic genera therefore represent only approximately 9% of the Antillean endemic species (Table IV). In addition, the 180 endemic genera account for only approximately 14% of all indigenous genera (Table IV).

Ninety-two of the endemic genera are unispecific (51%), and 30 (16%) of them have only two species (Tables III and IV). Therefore, the vast majority (122) of the endemic genera (approximately 68%) have two species or less. The five genera with the highest numbers of species are *Wallenia* (40 spp.), *Calycogonium* (36 spp.), *Dendropemon* (36 spp.), *Leucocroton* (28 spp.), and *Scolosanthus* (27 spp.) (Table I). There are at least 12 nonendemic genera that have more than 60 endemic species each (Howard, 1973). Therefore, none of the genera that have the highest number of endemic species are entirely endemic to the Caribbean Islands.

We investigated the phylogenetic positions of the endemic genera in the tree of life of seed plants using the phylogeny recently published by Soltis et al. (2005) (Fig. 2). Two lineages of basal angiosperms, monocots and Piperales (*Verhuellia*), have endemic genera



**Fig. 2.** Phylogenetic arrangement of the 180 seed plant genera endemic to the Antilles. Topology redrawn from Soltis et al. (2005). Lineages with endemic genera in the Antilles are indicated with open circles, and numbers inside circles indicate the number of genera endemic to the Caribbean Islands. Lineages with endemic families in the neotropics are indicated with arrows; those with endemic genera in the neotropics are indicated with solid circles; and those with endemic species in the neotropics are underlined.

(25) in the Antilles (Fig. 2). There are no endemic genera in the “Early-Diverging Eudicot” clade, and therefore the remaining 154 endemic genera of the flowering plants belong to the “Core Eudicot” clade. They are distributed in the asterids (103 genera), rosids (45 genera), Caryophyllales (five genera), and Santalales (one genus, *Dendropemon*). The “Core Eudicot” clade also has most of the plant biodiversity in the neotropics (Smith et al., 2004d). However, seven of the major lineages illustrated in Figure 2 have genera endemic to the neotropics but do not have any genus restricted to the Caribbean Island Hotspot.

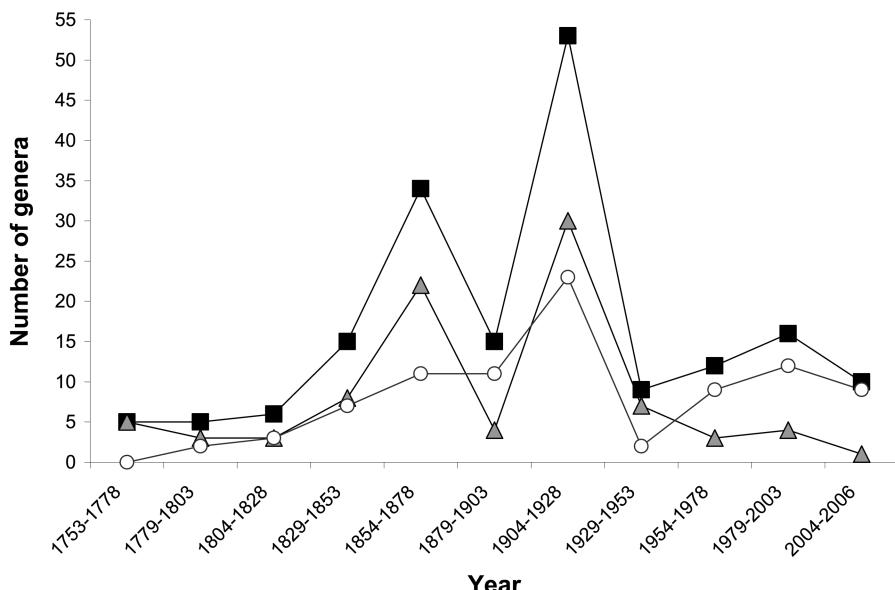
#### HISTORICAL PROFILE

Approximately half of the endemic genera (88: 49%) were published in two time periods 1854–1878 (34 genera) and 1904–1928 (54 genera) (Table I, Fig. 3). In terms of the number of endemic genera published, these two periods can be considered to represent the “golden age” of botanical exploration in the Caribbean Island Hotspot.

The first period was marked by the efforts of the North American plant explorer Charles Wright, who collected extensively in Cuba between 1856 and 1866; most of this material was subsequently studied and published by the German August Grisebach (León, 1946; Grisebach, 1860, 1862, 1866). Grisebach published 23 of the endemic genera during 1851–1877 (Table I). However, the second period (1904–1928) was that with the greatest activity. During that time 54 genera were published, mostly as the result of work by the German botanist Ignatz Urban, who between 1898 and 1928 published the nine-volume “Symbolae Antillanae” (Urban, 1898–1900, 1900–1901, 1902–1903, 1903–1911, 1904–1908, 1909–1910, 1911–1913, 1920–1921, 1923–1928). Approximately half of the descriptions of genera by Urban were based on collections made by the Swedish botanist Erik Leonard Ekman, one of the most prolific plant collectors of the region. Between 1914 and 1931, Ekman collected approximately 100,000 specimens from Cuba and Hispaniola (Howard, 1996; Mejía et al., 2001). Besides the endemic genera, Grisebach and Urban described many endemic species, including at least 25 genera that are not any longer regarded as endemic to this hotspot (Table II). Therefore, these two botanists have heavily influenced our current perception of taxonomic circumscriptions and, thus, plant biodiversity in the Antilles.

Most of the endemic genera were published between the second half of the nineteenth and the first half of the twentieth centuries, long before systematics and phylogenetics merged to provide tools for plant classification. Thirty-eight of the endemic genera (21%) were published after 1950, and the 10 most recently published (i.e., *Antillanthus*, *Atopoglossum*, *Elekmania*, *Herreranthus*, *Ignurbia*, *Leonis*, *Lundinia*, *Nesampelos*, *Salcedoa*, and *Zemisia*) were described between 2004 and 2006 (Jiménez-Rodríguez et al., 2004; Luer, 2004; Nordenstam, 2006a, 2006b). The 1979–2003 period was the third most active with respect to the number of published endemic genera (16 genera). However, most of the descriptions of these genera are new circumscriptions based on material collected prior to 1950; therefore, their basionyms were published much earlier. Only eight of 38 genera described between 1950 and 2006 are based on material collected after 1950 (i.e., *Acanthodesmos*, *Anacaona*, *Braasiella*, *Caribea*, *Kodialyodendron*, *Quisqueya*, *Salcedoa*, and *Seymeriopsis*) (Fig. 3).

A cumulative analysis of the chronology of discovery of endemic genera in the Caribbean Islands (Fig. 4) suggests that new genera created from taxonomic revisions are steadily increasing. New genera obtained from recent field explorations have decreased, and their publication is possibly approaching saturation. These results show



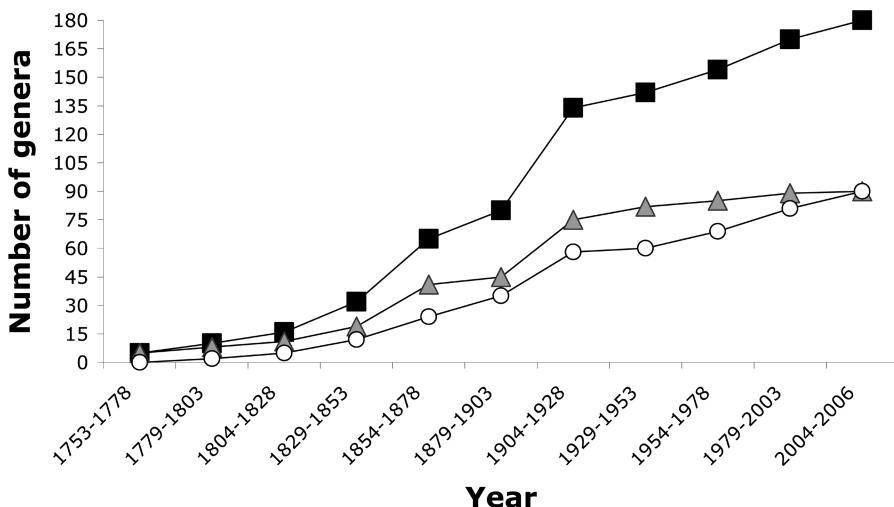
**Fig. 3.** Publications during 25-year intervals on the 180 genera endemic to the Caribbean Island Hotspot. Solid squares, total number of genera; gray triangles, genera whose original descriptions and/or type species were not based on a species previously described in another genus; open circles, genera whose descriptions and/or type species were based on a species previously described in another genus.

that botanical explorations conducted before 1950 may have already yielded most of the endemic diversity available at the generic level.

While most of the generic discoveries have apparently been made, we believe that there are still large collecting gaps in the region. On the island of Hispaniola, for instance, it is known that collection coverage in Haiti has not improved since 1989 (Zanoni, 1989). From our own research experience, we know that many endemic species reported for Haiti are known only from old herbarium collections, several dating back to Ekman's exploration days. Likewise, the karst hills ("mogotes") and the dry forests of the Dominican Republic, especially areas of the Barahona Peninsula and the Llanura Costera are in urgent need of collection (Ricardo García, pers. comm.; Zanoni 1989). George Proctor (pers. comm.) estimates that less than one quarter of the karst hills of Jamaica (especially the Cockpit Country) has been explored. Clearly, our numbers are subject to refinement from future collecting efforts that encompass these remote and topographically difficult areas.

#### COMPARISONS WITH OTHER INSULAR HOTSPOTS

Tables III and IV provide summaries of endemic seed plant genera for the Antilles and 19 additional islands/archipelagos. Results for the Malesian Islands (as geographically defined by Johns, 1995a) and Madagascar need to be interpreted with caution, as these two regions' floras are not fully understood yet (Johns, 1995a; Gautier & Goodman, 2003). In addition, data for these two island systems are for vascular or flowering



**Fig. 4.** Cumulative publications during 25-year intervals for the 180 genera endemic to the Caribbean Island Hotspot. Solid squares, total number of genera; gray triangles, genera whose original descriptions and/or type species were not based on a species previously described in another genus; open circles, genera whose descriptions and/or type species were based on a species previously described in another genus.

plants and not specifically for seed plants. We did not find data on the total number of species within endemic genera for Madagascar. Finally, there are no estimates of the total number of indigenous genera for four of the island systems included in our survey (Table III). Despite these limitations, we have estimates for the total number of endemic genera for the islands listed in Tables III and IV, and some comparisons can be made between the Antilles and other islands/archipelagos worldwide.

The Antilles rank third in number of endemic genera among the island systems included in our study. Only the Malesian Islands (at least 382 single-island endemic genera) and Madagascar (260 genera) have more endemic genera than the Antilles. The high proportion of unispecific endemic genera detected in the Antilles (51%) is also found in the rest of the island systems, with the exception of Hawaii (19%) and New Caledonia (44%) (Table IV). In addition, the only genus endemic to the Cape Verde Islands, *Tornabenea* Parl. (Apiaceae), is not unispecific but has five species (Brochmann et al., 1997). The Antilles have a low proportion of endemic genera (14%) and of species within the endemic genera (9%). With the exception of Borneo, none of the other island systems have more than 50% of their indigenous species within endemic genera (Table IV).

One of the major differences between the Antilles and other tropical insular systems concerns the distribution of endemic genera in the seed plant phylogeny recently published by Soltis et al. (2005) (Fig. 2). For instance, both Madagascar and the Malesian Islands have endemic genera in two of the major lineages of the magnoliids: Magnoliales and Laurales (Cronquist, 1981; Johns, 1995b; Soltis et al., 2005). The Antilles, on the other hand, have only one endemic genus (*Verhuelia*) belonging to one of these two major lineages.

The Canellales have at least one genus, *Takhtajania* Baranova & J-F.Leroy (Winteraceae), endemic to Madagascar (Cronquist, 1981; Soltis et al., 2005). The genus *Pleodendron* (Baill.) V. Thieghem, a member of the Canellales long considered an Antillean endemic, has recently been discovered in Central America (Hammel & Zamora, 2005). This finding restricts endemism of Antillean genera in the early branches of the angiosperms to *Verhuellia*, a genus with two species in Cuba and Hispaniola (Table II).

The “Early-Diverging Eudicot” clade does not include any Antillean endemic genera. In contrast, two of the five lineages of this paraphyletic group have endemic genera in Madagascar or the Malesian Islands. Malagasy and Malesian genera are found within the Ranunculales (Johns, 1995b; Soltis et al., 2005), whereas the Proteales have at least one genus, *Malagasia* L. A. S. Johnson & B. G. Briggs (Proteaceae), endemic to Madagascar (Johnson & Briggs, 1975; Soltis et al., 2005). Within the “Core Eudicots,” Madagascar and the Malesian Islands, as well as the Antilles, have endemic genera within the asterids, rosids, and Santalales. The Caryophyllales do not have any genus endemic to the Malesian islands, although both the Antilles and Madagascar have genera within this group. Only one gymnosperm genus is endemic to the Malesian Islands, *Papuacedrus* Li (Cupressaceae) (Page, 1998). Madagascar does not have any endemic gymnospermous genera.

The Caribbean Islands have a relatively recent geological history compared with that of most of the large continental islands of the Pacific and Indian oceans, such as Madagascar, New Zealand, New Caledonia, New Guinea, and the Fiji Islands (Nunn, 1994). The age of a great proportion of the land masses of these Old World islands predate the origin of the angiosperms. Therefore, it is not surprising that few of the early-diverging angiosperm lineages have any genus endemic to the Antilles and that one of the earliest branches of the flowering plants, the Amborellaceae, is endemic to New Caledonia. This phylogenetic pattern is also followed by the Trimeniaceae, a basal angiosperm family restricted to Sulawesi, eastern Australia, and the southwest Pacific, and by three of the six plant families of the Magnoliales (i.e., Degeneriaceae, Eupomatiaceae, and Himantandraceae). These three families are confined to Australia and/or the nearby Pacific islands (Carlquist, 1965; Soltis et al., 2005). In conclusion, we believe that the paucity of Antillean taxa in the early branches of the phylogeny of seed plants reflects the relatively recent evolutionary history of the biota of the region.

## Molecular Phylogenetics: Origin and Evolution of Antillean Genera

### MOLECULAR PHYLOGENETIC PATTERNS

#### *Sampled Taxa, Quality of Phylogenies, and Topology Features*

Information on phylogenetic patterns of 63 of the Caribbean Island endemic genera can be found in 50 papers on molecular phylogenetics (Table V). Therefore, there are DNA phylogenies available for only 35% of the Antillean genera. The vast majority of these phylogenetic studies (84%) aimed to elucidate generic relationships within particular families, tribes, or other suprageneric ranks, rather than to interpret phylogenetic patterns of any specific Antillean genus. Phylogenies for only 10 endemic genera (i.e., *Charianthus*, *Coeloneurum*, *Espadaea*, *Goetzea*, *Hebestigma*, *Henoonia*, *Pictetia*, *Poitea*, *Portlandia*, and *Rhodogerion*) have had as a primary objective to understand the

**Table V**

Molecular phylogenies that have included Caribbean Island genera. References on suprageneric classification are listed in Table I. Genera that are sister to other endemic genera indicated with an asterisk. The 21 genera that have molecular phylogenies (1) with well-supported relevant clades, (2) based on more than one independent DNA region, and (3) with good taxonomic sampling of their potential relatives are in bold print.

Genus	Suprageneric classification <sup>a</sup>	Sister taxon/clade	Distribution of sister taxon/ clade and notes	Reference
<i>Acidocroton</i>	Tribe Codiaeae (2/16; 1/10)	<i>Ophellanthia</i> Standl.	Genus from Central America to Colombia with 2 spp.; both were studied	Berry et al., 2005
<i>Arcea</i>	<i>Umitza</i> clade (3/7; 1/1)	Polytomy with three additional lineages. One of them with 20 genera <i>Pheidonocarpa</i>	Undetermined	Wojciechowski et al., 2004 <sup>b</sup>
* <i>Bellonia</i>	Uncertain tribal placement in Gesnerioid group (40/53; 1/2)	Polytomy with <i>Grimmeodendron eglandulosum</i> (A. Rich.) Urb and <i>Sebastiania bilocularis</i> S. Watson	Cuba and Jamaica Nested in clade with six additional spp. endemic to the Antilles <i>Grimmeodendron</i> (Antilles, 2 spp.; 1 was studied); <i>Sebastiania</i> Sprengel (neotropical, 25 spp.; 7 spp. were studied); <i>S. bilocularis</i> (North America)	Roalson et al., 2005; Smith et al., 2004a, 2004b Wurdack et al., 2005 <sup>b</sup>
<i>Bonania</i>	Subtribe Hippomaniae, tribe Hippomaneeae (23/33; 1/18)		Antillean. For further details see <i>Tetramicra</i> entry in Table V	Van Den Berg et al., 2000, 2005
* <i>Broughtonia</i>	Subtribe Laeliinae, tribe Epidendreae (41/43; 4/6)	<i>Psychilis</i>	Brazilian genus with 3 spp.; 1 was studied	Lavin et al., 2001a; Wojciechowski et al., 2004
<i>Brya</i>	Tribe Dallbergieae (44/49; 2/4)	<i>Cranocephalus</i> Benth.		
<i>Calycogonium</i>	Tribe Miconiaeae (20/38; 1/36)	Polytomy with four additional lineages <i>Tetrazygia</i> Rich, <i>Leanandra lima</i> (Desr.) Judd & Stean, and <i>Charianthus</i>	Clade restricted to Antilles and South Florida; Raddi (New World, 200 spp.; 6 spp. were studied)	Michelangeli et al., 2004 <sup>b</sup> (continued)

Table V (continued)

Genus	Suprageneric classification <sup>a</sup>	Sister taxon/clade	Distribution of sister taxon/ clade and notes	Reference
* <i>Ceratopyxis</i>	Catesbeiae-Chiococceae complex (24/28; 1/1) Tribe Miconiae (20/38; 6/6)	<i>Phialanthus</i> <i>Leandra lima</i>	Antilles. This clade is sister to Antillean genus <i>Schmidtia</i> Cuba and Hispaniola. Neotropical genus with 200 spp.; 6 spp. were studied	Rova et al., 2002; Motley et al., 2005 <sup>c</sup> Penney & Judd, 2005; Michelangeli et al., 2004b <sup>e</sup>
<i>Charianthus</i>			Mexico to Brazil, 5 spp., 2 spp. were studied	Wurdack et al., 2004 <sup>b</sup>
<i>Chascothecea</i>	Subtribe Pseudolachnomytidinae, tribe Phyllantheae (4/6; 1/3)	<i>Astrocasia</i> Robinson & Greenman	Antilles. This clade is sister to the Brazilian unspecific genus <i>Menterichia</i> Mik.	Santiago-Valentín & Olsmeid, 2003
* <i>Coeloneurum</i>	Subfamily Gotzeoideae (6/6; 1/1)	Clade with <i>Goetzea</i> , <i>Henoonia</i> , and <i>Espadacea</i>	Central America, Antilles, and Florida. See <i>Isidorea</i> entry in Table V	Brenner et al., 1995; Rova et al., 2002; Motley et al., 2005
<i>Cubanola</i>	Catesbeiae-Chiococceae complex (24/28; 1/2)	Clade with <i>Osa</i> , <i>Isidorea</i> , <i>Catesbeaea</i> , <i>Portlandia</i> , and <i>Phyllacanthus</i>	The Bahamas. Genus with 2000 spp.; 8 spp. were studied	Wurdack et al., 2005 <sup>b</sup>
<i>Cubanthus</i>	Subtribe Euphorbiinae, tribe Euphorbieae (6/8; 1/3)	<i>Euphorbia gymnantha</i> Urb. <i>Oryctanthus occidentalis</i> (L.) Eichl. <i>Neocogniauxia</i>	Neotropical genus with 10 spp.; 1 was studied	Nickrent & Duff, 1996 <sup>e</sup>
<i>Dendropemon</i>	Loranthaceae (23/75; 1/20)		Antilles. This clade is sister to a clade with seven genera with a widespread distribution in the neotropics	Cameron et al., 1999; Van Den Berg et al., 2000; 2005; Pridgeon et al., 2001; Freudenstein et al., 2001, 2004
* <i>Ditomilis</i>	Subtribe Laelliinae, tribe Epidendreae (41/43; 1/5)		South and Central America. Genus (Africa and neotropics) with 20 spp.; 3 spp. were studied	Wurdack et al., 2005 <sup>b</sup>
<i>Ditta</i>	Subtribe Adenoclininae, tribe Adenoclininae (5/5; 1/1)	<i>Tetrorchidium macrophyllum</i> Müll.	Brazilian unspecific genus <i>Nagellella</i> L.O. Williams	Richardson et al., 2000 <sup>b</sup> Van Den Berg et al., 2000 <sup>b</sup>
<i>Doerpfeldia Domingoa</i>	Rhamnaceae (41/52; 1/1) Subtribe Laelliinae, tribe Epidendreae (41/43; 1/2)	<i>Ampeloziphus</i> Ducke	Genus from Central America and Venezuela with 2 spp.; both were studied	Santiago-Valentín & Olsmeid, 2003
* <i>Espadacea</i>	Subfamily Gotzeoideae (6/6; 1/1)	<i>Goetzea</i>	Antilles. The Brazilian unspecific genus <i>Menterichia</i> is the closest continental relative	

<b>Fuentesia</b>	Loasaceae (17/20; 1/1)	<i>Gronovia scandens</i> L.	North, Central, and South America. Genus has 2 spp.; 1 was studied	Moody et al., 2001; Hufford et al., 2003
* <i>Goetzea</i>	Subfamily Gotzeoideae (6/6; 2/2)	<i>Espadaea</i>	Polytomy with <i>Bonania cubana</i> A. Rich. and <i>Sebastiania bilocularis</i> S. Watson	Santiago-Valentín & Olmstead, 2003
<i>Grimmeodendron</i>	Subtribe Hippomaniae, tribe Hippomaneeae (23/33; 1/2)		(neotropical, 25 spp.; 7 spp. were studied); <i>S. bilocularis</i> (North America)	Wurdack et al., 2005 <sup>b</sup>
<i>Haemianthus</i>	Subtribe Oleinae, tribe Oleaceae (12/12; 2/2)		Undetermined	Wallander & Albert, 2000 <sup>b</sup>
* <i>Harnackia</i>	Tribe Tageteae (23/23; 1/1)		Cuba. The clade <i>Lescaillea-Harnackia</i> is sister to the Mexican genus <i>Boeberastrum</i> (A. Gray) Rydb. (2 spp., 1 was studied)	Loockerman et al., 2003 <sup>b</sup>
<i>Hebestigma</i>	Tribe Robinieae (11/11; 1/1)	<i>Lennea</i> Klotsch	Mexican and Central American genus (3 spp.; all were studied)	Lavin & Doyle, 1991; Lavin et al., 2001b, 2003;
* <i>Henoomia</i>	Subfamily Gotzeoideae (6/6; 1/1)	Clade with <i>Goetzea</i> and <i>Espadaea</i>	Antilles. The Brazilian unspecific genus <i>Menemichia</i> is the closest continental clade	Wojciechowski et al., 2004
* <i>Isidorea</i>	Catesbeiae-Chiococceae complex (24/28; 5/17)	<i>Portlandia</i>	Antilles. This clade forms a polytomy with <i>Osa Aiello</i> (Central America, unspecific) and <i>Catesbeia</i> L. (Florida and the Antilles, 16 spp.; 4 spp. were studied)	Santiago-Valentín & Olmstead, 2003
<i>Lasiocroton</i>	Tribe Adelieae (4/5; 1/5)	Polytomy with <i>Leucocroton</i> and <i>Adelia ricinella</i> L.	<i>Leucocroton</i> (Antilles); <i>Adelia</i> L. (neotropical, mostly Antilles, 13 spp.; 1 was studied); <i>A. ricinella</i> (Antilles and South America)	Wurdack et al., 2005 <sup>b</sup>
<i>Leptocereus</i>	Tribe Echinocereeae (4/5; 1/12)	Polytomy with 10 additional genera	North, Central, and South America	Nyffeler, 2002 <sup>b,c</sup>

(continued)

Table V (continued)

Genus	Suprageneric classification <sup>a</sup>	Sister taxon/clade	Distribution of sister taxon/clade and notes	Reference
* <i>Lescaillea</i>	Tribe Tageteae (23/23; 1/2)	<i>Harmackia</i>	Cuba. The clade <i>Lescaillea-Harmackia</i> is sister to the Mexican genus <i>Boeherastrum</i> (2 spp.; 1 was studied)	Loockerman et al., 2003 <sup>b</sup>
<i>Leucocroton</i>	Tribe Adeliae (4/5; 1/28)	Polytomy with <i>Lasiocroton</i> and <i>Adelia ricinella</i>	<i>Lasiocroton</i> (Antilles); <i>Adelia</i> L. (neotropical, mostly Antilles, 13 spp.; 1 was studied); <i>A. ricinella</i> (Antilles and South America)	Wurdack et al., 2005 <sup>b</sup>
* <i>Mazaea</i>	Tribe Rondeletieae (1/5/30; 2/2)	<i>Phyllomelia</i>	Antilles. The clade <i>Phyllomelia-Mazaea</i> forms a polytomy with three additional lineages (3 genera)	Rova et al., 2002 <sup>b</sup>
<i>Mercurium</i>	Tribe Miconieae (20/38; 1/23)	<i>Miconia spinulosa</i> Naudin and <i>M. umbranoides</i> Naudin	North of South America. Genus has 1000 spp.; 25 spp. were studied	Michelangeli et al., 2004b <sup>b,c</sup>
<i>Microcytas</i>	Suborder Zamiineae (9/9; 1/1)	<i>Zamia</i> L.	North, Central, and South America. Genus with 40 spp.; 16 spp. were studied	Hill et al., 2003; Bogler & Francisco-Ortega, 2004; Chaw et al., 2005
<i>Macrocarpon</i>	Tribe Crotonae (7/7; 1/8)	<i>Croton olivaceus</i> Müll.	South America. Genus with widespread distribution, 2000 spp.; 83 spp. were studied	Wurdack et al., 2005 <sup>b</sup> ; Berry et al., 2005 <sup>c</sup>
* <i>Neocogniauxia</i>	Subtribe Laeliinae, tribe Epidendreae (41/43; 2/2)	<i>Ditomilis</i>	Antilles. This clade is sister to a clade with seven genera with a widespread distribution in the neotropic	Van Den Berg et al., 2000, 2005
* <i>Neomezia</i>	Theophrastaceae (7/7; 1/1)	<i>Theophrasta</i>	Antilles. The clade <i>Theophrasta-Neomezia</i> forms a polytomy with six additional clades	Källersjö & Ståhl, 2003 <sup>b,c</sup>
<i>Petitia</i>	Subfamily Viticoideae (4/10; 1/2)	<i>Vitex agnus-castus</i> L.	<i>Vitex</i> L. (pan-tropical, 250 spp.; 1 was studied)	Wagstaff & Olmstead, 1997; Wagstaff et al., 1998 <sup>b</sup>

* <i>Pheidonocarpa</i>	Tribe Gesnerieae (3/3; 1/1)	<i>Bellonia spinosa</i> Swartz	Roalson et al., 2005
* <i>Phialanthus</i>	Catesbeiae-Chiococceae complex (24/28; 2/18)	<i>Ceratopyxis</i>	Cuba and Hispaniola. Nested in clade with 6 additional spp. endemic to the Antilles
<b><i>Phyllacanthus</i></b>	Catesbeiae-Chiococceae complex (24/28; 1/1)	Clade with <i>Osa</i> , <i>Isidorea</i> , <i>Catesbea</i> , and <i>Portlandia</i>	Antilles. This clade is sister to the Antilles
* <i>Phyllocladus</i>	Uncertain (?/2; 1/1)	<i>Mazaea</i>	Antillean genus <i>Schmidtorita</i> Central America, Antilles, and Florida. See <i>Isidorea</i> entry in Table V
<i>Picardaea</i>	Tribe Condamineae (8/12; 1/1)		Antilles. The clade <i>Phyllomelia-Mazaea</i> forms a polytomy with 3 additional lineages (3 genera)
<i>Pictetia</i>	Tribe Dalbergieae (44/49; 8/8)		Undetermined
<i>Platygyna</i>	Subtribe Traginiae, tribe Plukeneteiae (5/9; 1/7)		<i>Omocarpum</i> (Africa, 24 spp.; 21 spp. were studied); <i>Diphyesa</i> (Mexico, Central, and South America, 15 spp.; 7 spp. were studied)
<i>Poitea</i>	Tribe Robinieae (11/11; 11/12)	<i>Gitaria Pax</i> & Hoffm. and <i>Tragia</i> L.	<i>Gitaria</i> (Central America and northern South America, 2 spp.; 1 was studied); <i>Tragia</i> (pantropical, 150 spp.; 3 spp. were studied)
* <i>Portlandia</i>	Catesbeiae-Chiococceae complex (24/28; 7/7)	<i>Giltricia Kunth</i>	Mexico, Central and South America, 3 spp.; all were studied
* <i>Psychilis</i>	Subtribe Laeliinae, tribe Epidendreae (41/43; 2/15)	<i>Isidorea</i>	Antilles. This clade forms a polytomy with <i>Osa</i> (Central America, unispecific) and <i>Catesbea</i> (Florida and Antilles, 16 spp.; 4 spp. were studied)
			Antillean. For further details see <i>Tetramicra</i> in Table V
			Van Den Berg et al., 2000 <sup>b</sup>

(continued)

Table V (continued)

Genus	Suprageneric classification <sup>a</sup>	Sister taxon/clade	Distribution of sister taxon/ clade and notes	Reference
* <i>Quisqueya</i>	Subtribe Laeliinae, tribe Epidendreae (41/43; 1/4) Tribe Plutcheeae (43/68; 1/1)	Clade with <i>Broughtonia</i> and <i>Psychilis</i> <i>Sachisia</i>	Antillan. For further details see <i>Tetramicra</i> in Table V Greater Antilles and Florida	Van Den Berg et al., 2000 <sup>b,c</sup>
<i>Rhodogerion</i>	Subtribe Diocleinae, tribe Phaseoleae (4/13; 1/2)	<i>Galactia tashiroi</i> Maxim.	<i>Galactia</i> P. Browne (widespread distribution, 60 spp.; 1 was studied); <i>G. tashiroi</i> (Asia)	Liu et al., 2004; Anderberg et al., 2005 <sup>b</sup>
<i>Roigella</i>	Tribe Rondeliteae (15/30; 1/1)	Polytomy with 3 additional lineages (4 genera)	Neotropical	Rova et al., 2002 <sup>b,c</sup>
<i>Sapixantha</i>	Tribe Acantheae (20/20; 1/1)	<i>Neriacanthus purdieanus</i> Benth.	Jamaica. This clade is sister to a lineage with two genera with a widespread distribution from Mexico to Argentina	McDade et al., 2005
* <i>Schmidtiottia</i>	Catesbeiae–Chiococceae complex (24/28; 1/16)	Clade with <i>Phialanthus</i> and <i>Ceratopryxis</i>	Antilles. This clade forms a polytomy with three other lineages (9 genera)	Rova et al., 2002; Motley et al., 2005
<i>Scolosanthus</i>	Catesbeiae–Chiococceae complex (24/28; 3/20)	Polytomy with two other clades: <i>Salzmannia</i> DC. and <i>Erithalis</i> P. Br.	<i>Salzmannia</i> (South America, unspecific); <i>Erithalis</i> (Antilles, and South America, 6 spp.; 3 spp. were studied)	Rova et al., 2002; Motley et al., 2005 <sup>c</sup>
<i>Sellcophytum</i>	Tribe Coreopsidae (13/25; 1/1)	<i>Naryalina domingensis</i> (Cass.) Less.	Hispaniola. Genus with 4 spp.; 1 was studied. This clade is sister to a lineage with the Polynesian genera <i>Fitchia</i>	Kimball & Crawford, 2004 <sup>b</sup>
<i>Siemensia</i>	Catesbeiae–Chiococceae complex (24/28; 1/1)	<i>Bilkka</i> Reinw. (3 spp. from New Caledonia) and <i>Morierina</i> Vieill.	<i>Bilkka</i> (Western Pacific and New Caledonia, 21 spp.; 7 spp. were studied); <i>Morierina</i> (New Caledonia, unispecific)	Rova et al., 2002; Motley et al., 2005 <sup>c</sup>
<i>Stahlia</i>	<i>Caesalpinia</i> group, tribe Caesalpiniaceae (16/21; 1/1)	Part of polytomy with 17 other lineages	Worldwide	Simpson et al., 2003 <sup>b,c</sup>

<i>Stempelioptis</i>	Tribe Alstoniaeae (9/9; 1/2)	Clade with <i>Haplophyton</i> A. DC. and <i>Vallesia Ruiz &amp; Pav.</i>	<i>Haplophyton</i> (North America, Antilles, 3 spp.; 1 was studied); <i>Vallesia</i> (neotropics, 8 spp., 1 was studied)	Potgieter & Albert, 2001 <sup>b</sup>
<i>Suberanthus</i>	Tribe Cinchoneae (13/37; 2/7)	Polytomy with 3 additional lineages (8 genera) Clade with <i>Broughonia</i> , <i>Psychilis</i> , and <i>Quisqueya</i>	Neotropical	Rova et al., 2002 <sup>b</sup>
* <i>Tetramicra</i>	Subtribe Laeliinae, tribe Epidendreae (4/14; 3; 1/15)		Antillean. This Antillean clade is sister to a large clade with most of the genera of the subtribe	Van Den Berg et al., 2000 <sup>b</sup>
* <i>Theophrasta</i>	Theophrastaceae (7/7; 1/2)	<i>Neomezia</i>	Antilles. The clade <i>Theophrasta</i> - <i>Neomezia</i> forms a polytomy with six additional clades	Källersjö et al., 2000; Mast et al., 2001; Bremer et al., 2002;
<i>Thymopsis</i>	Tribe Heleneiae, subtribe Chaenactidina (22/25; 1/2)	<i>Hymenopappus</i> L'Her.	North American genus with 14 spp., 2 spp. studied	Källersjö & Ståhl 2003 <sup>b,c</sup> ; Baldwin et al., 2002 <sup>b,c</sup>

<sup>a</sup> Figures in parenthesis indicate number of genera included in phylogeny/total number of genera in suprageneric taxon; number of species of endemic genus included in phylogeny/total number of species in suprageneric taxon.

<sup>b</sup> Results based on only one independent DNA marker.

<sup>c</sup> Bootstrap/jackknife support for relevant nodes <75%.

<sup>d</sup> Genus included in study by Herendeen et al. (2003). This phylogenetic study was based on combined molecular and morphological data.

<sup>e</sup> Unreported bootstrap/jackknife values.

origin and evolution of particular Antillean genera (Lavin, 1993; Beyra-Matos & Lavin, 1999; Lavin et al., 2001b, 2003; Delprête & Motley, 2003; Santiago-Valentín & Olmstead, 2003; Liu et al., 2004; Penneys & Judd, 2005). Phylogenies provided by Graham (2003c) and Herendeen et al. (2003) for *Haitia* and *Arcoa*, respectively, did not include reconstructions based on molecular data alone.

The five families with the highest number of endemic genera are well represented in molecular phylogenetic studies, with the exception of the Asteraceae. There are DNA phylogenies available for only five of the 31 endemic genera of the Compositae (i.e., *Harnackia*, *Lescaillea*, *Rhodogeran*, *Selleophytum*, and *Thymopsis*; Table I). Ninety percent of the Euphorbiaceae genera, and seven of the 10 Fabaceae genera, have been the subject of molecular phylogenetics. The proportion of Orchidaceae and Rubiaceae genera included in molecular phylogenies is 58% and 51%, respectively. There are no molecular phylogenies available for the Poaceae, a family with a relatively large number of endemic genera (nine) in the Antilles (Table V).

Molecular phylogenies of 16 of the endemic genera included less than 70% of the putative most closely related genera (Tables V, VI). Likewise, infrageneric sampling in 22 of the endemic genera that have more than two species each was less than 80%. Therefore, from these studies it is not certain whether the genera are monophyletic or not. Phylogenies of 36 genera are based on a single DNA region. In addition, DNA phylogenies of 15 genera display low bootstrap/jackknife support (<75%) for relevant nodes. Based on these data, only 21 genera have molecular phylogenies that (1) have well supported clades, (2) are based on more than one independent DNA region, and (3) have good taxonomic sampling of their potential relatives (Tables V, VI). These 21 endemic genera are indicated in bold print in Table V. The majority of the phylogenetic reconstructions were based on parsimony methods, and only 11 of these studies utilized model-based methods such as maximum likelihood or Bayesian analyses (i.e., Moody et al., 2001; Hufford et al., 2003; Smith et al., 2004a, 2004b; Kimball & Crawford, 2004; Wojciechowski et al., 2004; Berry et al., 2005; Van Den Berg et al., 2005; Wurdack et al., 2005).

Fourteen genera (i.e., *Arcoa*, *Bonania*, *Calycogonium*, *Grimmeodendron*, *Haenianthus*, *Lasiocroton*, *Leptocereus*, *Leucocroton*, *Picardaea*, *Platygyna*, *Roigella*, *Scolosanthus*, *Stahlia*, and *Suberanthus*) form polytomies with at least two additional lineages, and the closest relatives of these genera remain undetermined. In addition, 11 genera (i.e., *Charianthus*, *Cubanthus*, *Dendropemon*, *Ditta*, *Mecranium*, *Moacroton*, *Petitia*, *Rhodopis*, *Siemensia*, *Stempeliopsis*, and *Thymopsis*) are either sister to an assemblage that has a large number of continental genera or sister to a clade with very few representatives of a species-rich genus (Tables V, VI).

Only six of the endemic genera are early branches in their respective molecular phylogenies. For instance, the endemic radiation of *Broughtonia-Psychilis-Quisqueya-Tetramicra* (Orchidaceae) is sister to a major clade that includes three large generic alliances with species-rich genera such as *Epidendrum* L. and *Laelia* Lindl. (Table V). These four endemic genera form a monophyletic group that is an early branch in the subtribe Laeliinae (Van Den Berg et al., 2000, 2005). Likewise, the legumes *Arcoa* and *Hebestigma* represent early-diverging genera in the Caesalpinieae and Robinieae, respectively (Wojciechowski et al., 2004).

A similar pattern is followed by nine additional endemic genera, as they are part of early-diverging clades. However, these early-branching clades also include a small representation of continental genera. The subfamily Goetzeoideae is composed of the four

**Table VI**  
Summary of molecular phylogenies available

	Number of genera <sup>a</sup>
Bootstrap/jackknife support for relevant nodes >75%	48 (76%)
More than one independent DNA region included	27 (43%)
Sampling of putative continental relatives >70%	47 (75%)
Phylogenies with well supported clades, based on more than one independent DNA region, and good taxonomic sampling of putative relatives	21 (33%)
Genera that render other genera paraphyletic	6 (9%)
Genera that belong to radiations with more than one endemic genus	23 (36%)
Closest continental relatives in North America or North and Central America	9 (14%)
Closest continental relatives in South America or South and Central America	9 (14%)
Closest continental relatives in Old World	2 (3%)
Closest continental relatives have broad geographical distribution	43 (68%)

<sup>a</sup> Percentages calculated with respect to all 63 endemic genera.

endemic genera *Coeloneurum*, *Goetzea*, *Henoonia*, and *Espadaea*, plus three additional genera from South America and Madagascar. This subfamily is one of the earliest diverging lineages of the Solanaceae (Santiago-Valentín & Olmstead, 2003). Likewise, two of the earliest branching clades of the tribe Crotoneae include the endemic genera *Moacroton* and *Acidocroton* (Berry et al., 2005). The Greater Antillean orchid genera *Neocogniauxia* and *Dilomilis* belong to a clade with three additional mainland genera that is sister to the rest of the subtribe Pleurothallidinae (Van Den Berg et al., 2000, 2005; Pridgeon et al., 2001). Lastly, *Strempeliopsis*, together with five additional genera from the mainland, form a monophyletic group that is sister to the rest of the Apocynaceae (Potgieter & Albert, 2001).

Molecular phylogenies of at least six of the endemic genera [i.e., *Calycogonium*, *Charianthus*, and *Mecranium* (Michelangeli et al., 2004b), *Cubanthus* (Wurdack et al., 2005), *Domingoa* (Van Den Berg et al., 2000), and *Moacroton* (Berry et al., 2005)] raise questions about the generic status of these six taxa. Assigning them generic ranks will mean that closely related species-rich genera such as *Croton*, *Euphorbia*, *Laelia*, and *Miconia* become paraphyletic. We anticipate that it is likely that in the future the generic and suprageneric status of these endemic taxa will be reevaluated.

#### *Biogeographical Links with the Continent*

Table V provides information on the geographical distribution of those groups that are sister to the endemic genera. Three genera (i.e., *Acidocroton*, *Domingoa*, and *Scolosanthus*) are sister to genera restricted to South and Central America (Van Den Berg et al., 2000; Berry et al., 2005; Motley et al., 2005). Three of the Antillean genera (i.e., *Cubanola*, *Hebestigma*, *Phyllacanthus*) have their nearest relatives distributed in both North America and Central America (Levin et al., 2001b, 2003; Wojciechowski et

al., 2004; Motley et al., 2005). Two genera (i.e., *Brya* and *Doerpfeldia*) are sister to lineages in South America (Richardson et al., 2000; Lavin et al., 2001a, Wojciechowski et al., 2004). Only one genus, *Thymopsis*, is sister to a North American taxon, *Hymenopappus*. However, this relationship is supported by a low bootstrap value, and the study was based on a single DNA region from only one species of *Hymenopappus* (Baldwin et al., 2002). Likewise, only one genus, *Rhodogeran*, is sister to a genus endemic to the Antilles and North America, *Sachsia* (Liu et al., 2004; Anderberg et al., 2005). The closest relatives of 11 genera (i.e., *Bonania*, *Chascotheca*, *Fuertesia*, *Grimmeodendron*, *Lasiocroton*, *Leptocereus*, *Leucocroton*, *Microcycas*, *Poitea*, *Roigella*, and *Suberanthus*) have widespread distributions in North, Central, and South America (Lavin et al., 2001b, 2003; Moody et al., 2001; Nyffeler, 2002; Rova et al., 2002; Hill et al., 2003; Hufford et al., 2003; Bogler & Francisco-Ortega, 2004; Wurdack et al., 2004, 2005; Chaw et al., 2005). *Pictetia* is sister to a lineage that has taxa in both the New World and Africa (Lavin et al., 2001a, 2001b).

*Siemensia* is the only genus that has a sister relationship with a group from a remote region. This Cuban genus is sister to a clade of taxa restricted to New Caledonia; however, this relationship is supported by a low bootstrap value of 53% (Motley et al., 2005). A similar biogeographical pattern has also been reported for the Hispaniolan genus *Selleophyllum*, which forms a clade with the Hispaniolan species *Narvalina domingensis* (Cass.) Less. This clade is sister to a group composed of two Polynesian genera, *Fitchia* and *Oparanthus* (Kimball & Crawford, 2004).

*Salpixantha* is another genus that is sister to an Antillean endemic. The closest relative of this Jamaican taxon is the Jamaican endemic *Neriacanthus purdieanus*. This Antillean clade is sister to a clade with four species with a widespread distribution in the New World (McDade et al., 2005).

Several of the Antillean genera are sister to other endemic genera (Table V). We have identified nine lineages (23 genera and 123 spp.) composed exclusively of endemic genera. These nine lineages are *Bellonia-Pheidonocarpa* (3 spp.); *Broughtonia-Psychilis-Quisqueya-Tetramicra* (40 spp.); *Ceratopyxis-Phialanthus-Schmidtottia* (35 spp.); *Coeloneurum-Goetzea-Henoonia-Espadacea* (5 spp.); *Dilomilis-Neocogniauxia* (7 spp.); *Harnackia-Lescaillea* (3 spp.); *Isidorea-Portlandia* (24 spp.); *Mazaea-Phylloamelia* (3 spp.); and *Neomezia-Theophrasta* (3 spp.) (Table V). These nine monophyletic assemblages are supported by high bootstrap values; the only exceptions are the sister relationships between the *Ceratopyxis* and *Phialanthus* and between *Neomezia* and *Theophrasta* (Källersjö & Ståhl, 2003; Motley et al., 2005).

Five of these nine Antillean lineages collapse in polytomies with other lineages, or are sister to clades that have a widespread distribution. The five species of the *Coeloneurum-Goetzea-Henoonia-Espadacea* Antillean radiation provide an excellent example of a South American connection; this lineage is sister to the Brazilian genus *Mettnerichia*. This Antillean-Brazilian clade is sister to *Duckeodendron Kuhlm.*, a unispecific genus also endemic to Brazil (Santiago-Valentín & Olsmstead, 2003). In contrast, a connection with the North American flora is provided by the Cuban lineage *Harnackia-Lescaillea*, which is sister to the Mexican genus *Boeberastrum* (Loockerman et al., 2003). The *Isidorea-Portlandia* lineage is part of a clade that contains the unispecific genus *Osa* from Central America, and *Catesbaea*. The latter is confined to the Bahamas, the Greater Antilles, and South Florida (Motley et al., 2005). The *Bellonia-Pheidonocarpa* radiation falls in a clade that has four additional species endemic to the Greater Antilles (Roalson et al., 2005). This clade is supported by a 100% bootstrap value and is

sister to another large monophyletic group that has 13 genera and a widespread distribution.

In summary (Table VI), we found that nine (14%) of the endemic genera included in the phylogenetic studies are sister to groups with a North American or North American-Central American distribution. In addition, 14% of the endemic genera are sister to taxa from South America or South America-Central America. None of the endemic genera are sister to a Central American group. Likewise, none of the genera included in these phylogenetic studies are sister to an Old World lineage, with the exception of two genera (3%) that appear to be closely related to taxa confined to Pacific islands. However, most of the endemic genera (43, 68%) either collapse in a polytomy with several taxa with widespread distributions or are sister to clades with a broad geographical range.

#### DISCUSSION OF MOLECULAR PHYLOGENETIC PATTERNS

The Caribbean Islands have had a complex environmental history that has involved major eustatic/isostatic sea-level changes, climatic changes, volcanism, and migration of lithospheric plate boundaries (Iturralde-Vinent & MacPhee, 1999; Pindell & Kennan, 2001; Fritsch & McDowell, 2003). Environmental biologists agree that these environmental factors have had a tremendous impact on the biota of the Caribbean Island Hotspot, and it is likely that the islands have gone through several colonization and extinction waves (Iturralde-Vinent & MacPhee, 1999; Hedges, 2001).

The most accepted geological model for the region has the Greater Antilles originating in the early Cretaceous (~130 million years ago [mya]) as a volcanic chain of islands between North and South America in an area close to the present Panamanian Isthmus (see Pindell & Kennan, 2001; Pindell et al., 2005; Iturralde-Vinent, 2006). These islands are known as the Proto-Greater Antilles. They subsequently moved in a northeastward direction until they collided first with the Yucatan Peninsula (at about 84 mya) and then with the Bahamas platform in the early Eocene (~56 mya) (reviewed by Graham 2003a, 2003b). The origin of the Proto-Greater Antilles is linked to the opening of the Atlantic Ocean when South and North America separated (Pindell, 1994; López-Ramos, 2001). It is believed that by the middle Eocene (~49 mya), most of the Greater Antilles and part of the Lesser Antilles were above sea level as established pieces of landmass. It is suggested that prior to the middle Eocene the islands went through several emergence and submergence intervals, but it is only after this geological epoch that the Antilles started a period of “sustained emergence” (Graham, 2003a, 2003b).

According to this model, the middle Eocene is regarded as the starting point for the current fauna and flora of the Antilles (Iturralde-Vinent & MacPhee, 1999; Graham, 2003a, 2003b). Thus, the flora of the Caribbean Islands is relatively young when compared with that of South and North America. Support for the middle Eocene origin of the Antillean flora comes from the fossil record. The oldest fossil deposits in the Greater Antilles are in Cuba and Jamaica, and both date from this geological epoch (Graham, 1993; Graham et al., 2000). Graham (2003a) indicated that unpublished reports of terrestrial plant fossils from the Early Cretaceous found in Hispaniola need to be interpreted with caution, as the fossils are from areas overlaid by marine deposits of Albian age (99–112 mya).

The research of Lavin et al. (2001b, 2003) on the molecular systematics of the Antillean genera *Hebestigma*, *Pictetia*, and *Poitea* confirms this hypothesis, as these three taxa diverged from their sister groups in the Miocene. Ages of diversification of these

three genera were estimated using evolutionary rate analysis methods combined with information from the fossil record. Divergence times ranged between 35 and 9 mya for *Pictetia* and *Poitea*, respectively (Lavin et al., 2001b, 2003).

However, not all of the endemic genera seem to have originated after the middle Eocene. The Cuban genus *Microcycas* is extremely rare and sister to *Zamia* (Hill et al., 2003; Bogler & Francisco-Ortega, 2004; Chaw et al., 2005). The latter is the largest genus of the order Cycadales (~60 spp.), and it is found from Bolivia northward through tropical America to southeastern United States and the West Indies. There are lower Eocene (~55 mya) fossils of at least three species of *Zamia* (i.e., *Z. mississippiensis* E. W. Berry, *Z. tennesseana* E. W. Berry, *Z. wilcoxensis* E. W. Berry) (reviewed by Jones, 1993). This fossil record suggests that the split between *Microcycas* and *Zamia* occurred long before the middle Eocene. Hermsen et al. (2006) argued that this separation occurred in the Paleocene, although these authors also indicate that the fossil record for *Zamia* needs to be reinvestigated. These fossil data suggest that both genera may have originated on the mainland. *Microcycas* reached Cuba sometime after the middle Tertiary, before becoming extinct elsewhere. A second hypothesis is that some pockets of the Proto-Greater Antilles may have escaped the major environmental changes that occurred in these islands prior to the middle Eocene, and that *Microcycas* might have survived in some of these pockets. As indicated by Iturralde-Vinent (2004–2005), the paleogeography of the Caribbean Basin between the Cretaceous and the Upper Eocene is still difficult to interpret, and there are still disagreements among the several geological models concerning the tectonics of the region. It is at the end of the Cretaceous that the Yucatan area experienced an asteroid impact. There is disagreement among paleoecologists on the effects this catastrophic event had on the biota of the Antilles. Some specialists argue that this impact led to the virtual extinction of all of the biota of the Caribbean Island Hotspot (Hedges, 1996; Iturralde-Vinent, 2004–2005). Other authors disagree with this hypothesis and consider it unlikely that the asteroid collision produced massive extinction of Antillean organisms (Crother & Guyer, 1996).

Molecular phylogenetic studies for vertebrates also suggest a pre-middle Eocene origin for at least four endemic groups of tetrapods. Molecular divergence studies of the Antillean genus *Solenodon* J. F. Brandt (Insectivora), the frog *Eleutherodactylus* Duméril and Bibron, the lizard *Cricosaura* Gundlach and Peters, and the worm lizard *Amphisbaena* L. revealed that these taxa diverged long before the middle Eocene (Hedges, 1996; Hass et al., 2001; Roca et al., 2004). Some researchers, led primarily by S. B. Hedges, consider “recent” dispersal from the mainland during the Tertiary of now extinct continental animals as the best explanation for the occurrence of these ancient vertebrate lineages in the Antilles (Hedges, 1996; Hass et al., 2001). Other authors argue against this view and believe that some of these ancient lineages originated on the islands and survived the major environmental changes that have occurred in the region since the late Cretaceous (reviewed by Duellman, 1999; Pregill & Crother, 1999). Most of these authors also believe that a great proportion of the Antillean biota originated during late Cretaceous-early Paleocene land connections between Meso- and South America. These biogeographical links were provided by the Proto-Greater Antillean arc. It has been suggested that during that time this chain of volcanic islands was in close proximity to both Meso- and South America (Savage, 1982).

The phylogenetic patterns of *Microcycas* and some vertebrates may provide support for a hypothesis proposed by several island phytogeographers wherein in many instances ancient lineages currently extinct on the mainland have found shelter on

“young” islands (e.g., Sunding, 1979; Cronk, 1992, 1997). This view is supported by *Lactoris* Phil. (Lactoridaceae), a genus endemic to the island of Masatierra in Juan Fernandez archipelago. This island is only approximately 4 million years old (Stuessy et al., 1984). However, there are *Lactoris* fossils from South African upper Cretaceous deposits (Zavada & Benson, 1987).

The Caribbean Island Hotspot has a unique geographical situation, as it is located between two major continents: South and North America. The continents also represent two major potential sources for the biota of the hotspot. A primary Gondwana origin has been suggested for its biota through South America (e.g., Fig. 3 in Howard, 1973). However, other authors consider that many of the taxa of tropical North America, including those present in the Antilles, are linked to those that existed in Laurasia during the early Tertiary. At that time, there was a major global temperature increase known as the Eocene thermal maximum (reviewed by Lavin and Luckow, 1993). Gentry (1982) also stressed the importance of a Laurasian-derived versus Gondwanan-derived origin for the neotropical flora and indicated that this dichotomy is more obvious in the Caribbean Islands than in any other neotropical region.

Historical biogeography research coupled with molecular phylogenetics suggest that at least two of the endemic genera, *Pictetia* and *Poitea*, originally came from Tertiary North American groups (Lavin et al., 2001b). In contrast, similar studies conducted by Santiago-Valentín & Olmstead (2003) showed that the four endemic genera of the subfamily Goetzeoideae have their ancestors in South America. *Doerpfeldia* is another endemic genus that appears to have a Gondwana origin, as it is sister to the Brazilian *Ampeloziziphus*. These two genera are sister to *Bathiorhamnus* Capuron, a genus endemic to Madagascar (Santiago-Valentín & Olmstead, 2003).

Unfortunately, most of the molecular phylogenetic studies that include Antillean taxa lack any historical biogeography framework. For many of the endemic genera, we have identified the geographical area of their closest relative(s) (Table V); however, we still need further data to infer the geographical distribution of their ancestors. Nevertheless, based on the few examples indicated in our review, it appears that both Gondwana and Laurasia have been source areas for the islands. Recent data indicate that out of 11,440 seed plant taxa native to the Antilles, only 1237 (11%) belong to Laurasian plant families (Acevedo-Rodríguez & Strong, unpublished).

Molecular phylogenetic studies of other island systems, primarily the Macaronesian Islands, indicate that in several instances islands have acted as source areas for mainland biota (Andrus et al., 2004; Carine et al., 2004). Islands of this region are at close geographical distance from the mainland. This pattern has also been detected in the Antilles, where a molecular phylogeny and historical biogeography study of *Rhodogerion* and its closest relatives shows that the species of *Sachsia* occurring in Florida (i.e., *S. polyccephala* Griseb.) arose from Cuban ancestors (Liu et al., 2004). This pattern has also been reported for the Caribbean species of *Ernodea* (Rubiaceae) (Negrón-Ortiz & Watson, 2003) and for the lizard genus *Anolis* Daudin (Glor et al., 2005; Nicholson et al., 2005).

The Caribbean Islands follow a pattern detected in other tropical and subtropical archipelagos where several endemic genera group together and form monophyletic groups. These “radiation” groups provide evidence of the nature of adaptive radiation and morphological release that occurs on islands. Unusual morphological forms with unique adaptive value are expected to originate in highly disharmonic insular environments following establishment, colonization, and in situ evolution (Crawford et al., 1987; Givnish, 1998; Whittaker, 1998).

In the Atlantic Ocean, molecular phylogenies have identified at least four of these kinds of “generic radiations” in the Macaronesian islands: the *Aeonium* Webb & Berthel. alliance (Crassulaceae) (Mort et al., 2002); the woody *Sonchus* L. (Asteraceae) alliance (Lee et al., 2005), the *Bencomia* Webb & Berthel. Alliance (Rosaceae) (Helfgott et al., 2000), and genera of the Gonosperminae (Asteraceae), Francisco-Ortega et al., 2001). *Commidendrum* DC. and *Melanodendron* DC. (Asteraceae), endemic to the Atlantic island of St. Helena, also form a monophyletic group (Eastwood et al., 2004). In the Pacific Ocean, the silversword alliance (Asteraceae), *Schiedea* Cham. & Schltdl. (including *Alsinidendron* H. Mann) (Caryophyllaceae), and the Hawaiian lobelioids (Campanulaceae) are three good examples of generic diversification from the Hawaiian Islands (Soltis et al., 1996; Givnish, 1998; Baldwin, 2003; Wagner et al., 2005). Similar patterns have been found on the Indian Ocean islands, where the Socotran genera *Nirarathamnos* Balf.f. and *Rughidia* M. F. Watson & E. L. Barclay (Apiaceae) are sister genera (Downie et al., 2000). Likewise, four palm genera of the Seychelles island-endemic subtribe Verschaffeltiinae form a clade (Lewis & Doyle, 2002).

### Conclusions and Conservation Remarks

During the preparation of this paper, we realized that there is a paucity of studies focusing on the conservation biology of plants endemic to the Antilles. Available information on the conservation status of these plants is limited to the few taxa found in the Red List of Threatened Species of the World Conservation Union (IUCN, 2006) and in four publications on endangered plant species of Cuba and Jamaica (Borhidi & Muñiz, 1983; Kelly, 1988; Rankin-Rodríguez & Areces-Berazaín, 2003; Berazaín-Iturralde et al., 2005). The two most recent accounts are from Cuba, and the authors used the latest conservation categories and criteria developed by the World Conservation Union (IUCN, 2001). However, these two studies included only up to 20% of the flowering plants of this island. Introductory reviews on conservation aspects of Antillean plants are also scattered in several introductory papers on biodiversity of the Caribbean Islands (e.g., Howard, 1977; Adams, 1997; Smith et al., 2004c). We have also found additional data on the distribution patterns and conservation status of the endemic genera in taxonomic treatments/descriptions, as well as in regional floras. It is out of the scope of our paper to provide an exhaustive account of the current conservation status of the endemic genera. However, on the basis of our field experience and the information found in these sources we are certain that at least 17 of the unispecific genera are highly threatened (e.g., *Asciadium*, *Doerpfeldia*, *Euchorium*, *Euleria*, *Harnackia*, *Kodalyodendron*, *Lepthuridium*, *Microcycas*, *Nodocarpaea*, *Phyllacanthus*, *Rhodogeron*, *Salcedoia*, *Solonia*, *Stahlia*, *Synapsis*, *Tetrasiphon*, and *Tetraperone*). In addition, several of the genera with four or more species each have at least one threatened species each (e.g., *Gyrotaenia*, *Lasiocroton*, *Leptocereus*, *Leucocroton*, *Phialanthus*, and *Wallenia*). From our review it is clear that more comprehensive studies on the current distribution patterns and the conservation biology of the plant genera endemic to the Caribbean Islands are immediate priorities for the Caribbean Island Hotspot.

With the exception of the work by Lavin et al. (2001b, 2003), none of the molecular phylogenies have used evolutionary rates analysis methods to estimate ages of speciation events. Therefore, it is not certain how many of these genera have a post-middle Eocene origin, as demonstrated for *Hebestigma*, *Pictetia*, and *Poitea*, or how many of them may be much older, as shown for *Microcycas*. Many of the plant families repre-

sented by endemic genera in the Antilles seem to have diversified in the early Tertiary or late Cretaceous (Crapet et al., 2004; Magallón-Puebla & Sanderson, 2005); therefore, we cannot rule out that further phylogenetic and evolutionary divergence studies will reveal that *Microcycas* is not the only Antillean genus with a pre-middle Eocene origin. We have identified at least 10 endemic genera (i.e., *Acidocroton*, *Arcoa*, *Dilomilis*, *Broughtonia* alliance, *Moacroton*, *Neocogniauxia*, and *Strempeleopsis*) that belong to early divergent lineages of plant families dating to the Cretaceous or Paleocene (i.e., Apocynaceae, Euphorbiaceae, Fabaceae, and Orchidaceae) (Magallón-Puebla et al., 1999; Knapp, 2002; Crapet et al., 2004; Chase, 2005; Davis et al., 2005; Magallón-Puebla & Sanderson, 2005; Schrire et al., 2005). We are aware that there is controversy concerning the methods available to date nodes on phylogenetic trees (reviewed by Heads, 2005). Accurate dating of phylogenies is a difficult process, and the current methodology only provides the best possible approximation (Smissen et al., 2005). However, we are also aware that recent progress has been made in obtaining better estimates of times of divergence and identifying sources of error (Magallón-Puebla & Sanderson, 2005). Therefore, we believe that results from these analytical procedures can provide a valid temporal framework to better understand the major plant diversification events of the Caribbean Island Hotspot. We anticipate that this will be an expanding research area in the future.

Our review shows that families with relatively large numbers of endemic genera such as Asteraceae and Poaceae have been poorly studied. We also found that molecular reconstructions seem to be reliable for only one-third of the studied genera. These genera have molecular phylogenies that are based on good taxonomic sampling, used more than one independent molecular marker, and had strong support for relevant nodes. Therefore, several uncertainties remain concerning the interpretation of results from the remaining two-thirds of the endemic genera.

The 180 genera endemic to the Caribbean Island Hotspot should not only represent a front line for conservation biology in the region but also a major priority for future biodiversity studies. In this review we have shown how some of these genera are extremely rare, and how some of them represent unique lineages in the tree of life of seed plants. Future research needs to include genera from poorly represented families, and taxonomic sampling needs to be improved; an increased number of DNA regions should also be studied, with increased statistical support for relevant clades.

In the initial definition of biodiversity hotspots, the Caribbean Island Hotspot ranked as the fifth “hottest” in terms of five major biodiversity factors (Myers et al., 2000). Thus, it is clear that resources should be allocated to the preservation of the biota of this region according to three major priorities: (1) field studies to determine the conservation status of endemic genera; (2) effective protection of the habitats where the most endangered genera occur, along with implementation of any required species and habitat management; and (3) additional biological and systematic studies of the least understood genera.

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